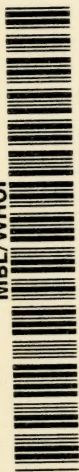




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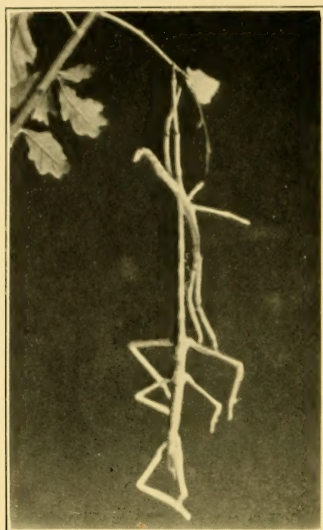
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# PLATE I



A. STICK-INSECT (*Carausius morosus*), JAVA, moulting while hanging from Oak-twig. Half size.

[J. H. Watson, photo.]



B. SNOWY-FLY (*Aleyrodes vaporarum*) ON LEAF.  $\times 10$ .  
Frontispiece.]

[H. Britten, photo.]



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2

# THE BIOLOGY OF INSECTS

BY

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THE BIOLOGY OF  
INSECTS



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TO  
MY WIFE  
AFTER THIRTY-SIX YEARS OF  
COMRADESHIP



## PREFACE

THE writer on Insects in this series of volumes, setting forth various groups of creatures from the biological point of view, has the advantage of his subject in a class of animals comprising the largest number of diverse forms whence he may choose examples of life relations. He has also the disadvantage which follows inevitably from this richness of the available material ; many highly interesting features of insect life must be neglected or treated inadequately if the book is to be kept within reasonable compass. He must therefore acknowledge himself chargeable with the offence of omitting many subjects which might be expected to appear in a survey of the Biology of Insects.

In this volume structural features are described only so far as seems necessary for the understanding of function and behaviour, while questions of systematic entomology are discussed only as they bear on problems of ecology and evolution. The author's indebtedness to those who have studied and written upon the various aspects of Insect Biology is apparent, and, he trusts, duly acknowledged, both in the text and in the descriptions of those photographs and figures which have been borrowed or copied for illustration. He desires to express gratefully his appreciation of the help and encouragement accorded by his friend, Professor J. Arthur Thomson, the editor of this series, whose suggestions and criticisms have contributed



largely to whatever value the book may have. It is a pleasure to acknowledge also the willing help of two friendly colleagues in the work of illustration: Miss R. A. Barr with her careful draughtsmanship and Mr. H. Britten with his taste and skill in nature-photography. Finally hearty thanks are due to the publishers for their patience and consideration through the prolonged fulfilment of the author's promise to take this part in their scientific enterprise.

G. H. C.

THE UNIVERSITY,  
MANCHESTER,  
*October, 1927.*

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# THE BIOLOGY OF INSECTS

## CHAPTER I

### INTRODUCTION

THE studies of an entomologist are often associated with long rows of dead, dried insects, set on pins or mounted on cards, arranged in a series of cabinets or storeboxes. Yet such a typical collection of beetles or butterflies is made up of creatures that once had life, and the opportunity which it affords for the examination and comparison of the forms of insect-bodies may help towards an understanding of the living insects which once flew or crawled, fed and breathed, mated and bred in the brightness of a summer's day. In the succeeding pages the attempt will be made from diverse points of view to demonstrate insects as living organisms.

In most groups of animals there are certain outstanding characteristics which determine to a great extent each creature's form of body and mode of life. The bird is feathered and flying, moulded as it were in clothing and manner of movement to the air. The typical worm is a crawler or burrower, compelled to seek shelter in soil or sand for its soft, ill-defended body. What then are the main features of an insect's body-structure which are correlated with its functions as a live being? Curiously enough the collection of dry pinned or carded specimens suggests the beginning of an answer. Insects can be preserved in this way because of the firmness of their outer

body-covering ; they belong to that great race<sup>1</sup> of animals among whose members the living skin (Fig. 1, *e*) forms outside itself a more or less firm and resistant cuticle, composed of a horny substance called chitin (the chemical composition of which has been represented by the formula  $C_{30}H_{50}O_{10}N_4$ ), and thickened segmentally in agreement with the marked segmentation of the body and limbs so as to build up a jointed exoskeleton. This coat of mail, as it may be somewhat fancifully termed, affords the living insect much protection from its enemies and also enables it to achieve

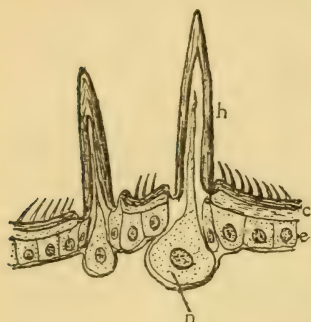


FIG. 1.—Section through cuticle (*c*) and skin or epidermis (*e*) of the leg-base of a Bluebottle (*Calliphora*) just after casting the pupal cuticle. *h*, sensory hair ; *n*, nerve-cell.  $\times 300$ .

great precision and rapidity of movement, since the muscles of the trunk and limbs are attached internally to the hard firm parts of the exoskeleton, which being united by tracts of flexible cuticle, move readily on one another. Further, it is noteworthy that in this great group of animals the muscle-fibres when viewed with the microscope, show the same kind of cross-stripping that characterises the body-muscles of vertebrates.

Other classes of animals besides insects are built on the general plan just described—spiders, centipedes, millipedes, lobsters and crabs for example. But while most of these have many pairs of jointed limbs adapted for crawling or swimming, insects generally have the legs reduced in number to six, and the great majority of them display a highly characteristic feature in the presence of two pairs of flattened outgrowths arising from the dorso-lateral region of two adjacent, forwardly situated body-segments (Fig. 2). These outgrowths, jointed on to the body and capable of depression and elevation by the action of suitable muscles

<sup>1</sup> The Arthropoda. See Classification, Chapter XI.

attached at or near their bases, are the wings—rigid enough, since they consist largely of firm cuticle, to support in the air the creature that bears them, so that insects are among the few groups of animals which possess the power of true flight ; like the birds they are moulded to the air. There are indeed many insects wingless or incapable of flight, the best known examples being such parasites as lice or fleas. But taking the class as a whole the wings are a dominant feature and flight is a characteristic activity, so that the vast

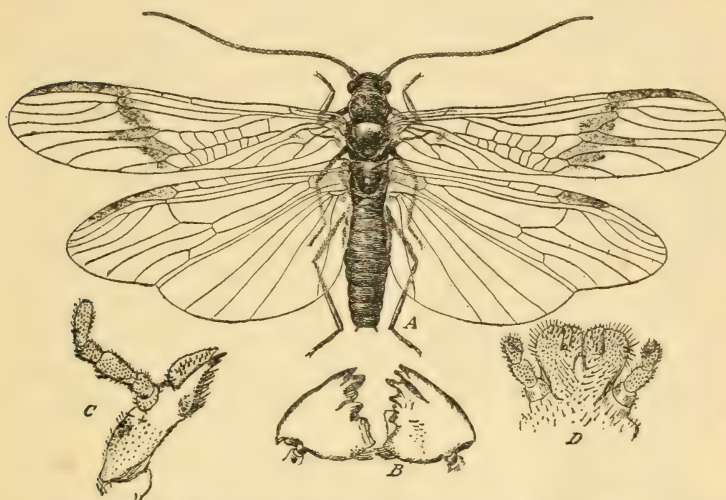


FIG. 2.—A, Stonefly (*Taeniopteryx pacifica*) North America,  $\times 5$  ; B, mandibles ; C, maxilla ; D, labium ;  $\times 25$ . From E. J. Newcomer, *Journ. Agric. Res.* (U.S.D.A.) xiii, 1918.

majority of insects may be regarded as segmentally built, armoured creatures, able not only with nice precision to walk or run, but to rise into and propel themselves through the air.

Such strenuous activity calls for a constant supply of energy. In all animals the source of the energy dissipated in motion, in the radiation of heat, or in other channels, must be sought in the highly complex chemical constitution of the living body-substance the food materials combined or in association with which are broken down by oxidation-



processes analogous to combustion or explosion. The animal body requires therefore a supply of oxygen to support this combustion-process, and a supply of food to provide for the repair of waste and to act the part of fuel in the living heat-engine. An animal that continues to live must feed and breathe. Now the organs and the method of breathing in insects are among the most markedly distinctive of the structural and vital features of this class of animals.

In several classes of the Arthropoda—the great comprehensive Group or Phylum to which insects belong—we find that the outer skin with its firm cuticle is pushed into the body in such a manner as to give rise to a series of branching air-tubes of which the firm cuticle necessarily forms the lining and prevents their channels from collapsing. As these air-tubes open to the outside through a set of breathing-holes or spiracles, air can pass in and come into touch with organs inside the creature's body so that the process of oxidation becomes easy and direct; the oxygen needs not the circulating fluid or blood to carry it from special breathing organs such as lungs or gills to the tissues where the combustion processes are constantly going on (Figs. 14, 15).

Air-tubes like those just described are found in centipedes, in certain spiders, and in many mites as well as in insects; but it is among the insects that we find them in the highest grade of development. In a typical aerial flying insect the spiracles are arranged segmentally in pairs along the sides of the body, while the tubes branch repeatedly, ending in minute ramifications with walls of exceeding delicacy which allow free gaseous exchange between the tissues and the atmosphere, oxygen being taken to support the combustion-processes while waste products—carbon dioxide and water-vapour—are given off. Such a flying insect, therefore, while it lives in the air and is bathed in it—using the aerial resistance for support and progress—is also permeated with air inwardly, illustrating as perhaps no other animal can do, the deeper meanings of that old-time



definition of living creatures : " in which is the breath of life."

Yet, though insects as a group are typically aerial, they afford many and remarkable adaptations to life in water ; especially noteworthy are those members of the class—dragonflies and gnats for example—which pass the early or preparatory stages of their lives in streams or ponds, emerging into the upper air as they acquire the wings whose full development marks always the attainment by an insect of the adult or perfect state. The various modifications connected with such aquatic modes of life will be considered later.

In turning from breathing to feeding, we fail to find a distinctive method of action for the class of insects generally. Indeed they are remarkable rather for the great variety displayed in the nature of their food and the means by which they procure it. With regard to the latter question, however, attention may suitably be drawn in this introductory sketch to a structural character common to insects and allied classes of the Arthropoda. This is the modification for feeding purposes of certain pairs of limbs that belong to those three or four segments of the body that make up the hinder region of the head (Figs. 2, *B, C, D* ; 6, 7, 8, 9). These limbs become wonderfully adapted for testing or tasting, for biting or piercing, for licking up or sucking in the widely different substances—such as the tissues or fluids of live plants and animals, the decaying remains of dead organisms—from which insects of different type draw their food supply.

One or two features in the digestive system of insects are also worthy of note. The outer skin with its secreted covering of cuticle is pushed inwards in such a way as to form the lining of two extensive tracts situated respectively at the front and hinder ends of the food canal ; these are the " fore-gut " and " hind-gut " of the arthropodous digestive tube. The " mid-gut," often comparatively restricted in length, is lined by a sheet of living cells uncoated with cuticle ; this cell-layer or epithelium elaborates the juices with their digestive ferments which act upon the

food (Figs. 10, 11). Such action may go on in the fore-gut or hind-gut also, by the transference thither of portions of food mingled with the juices, and the digested food-material may be absorbed through the thin cuticle lining those regions of the canal, and so traverse their wall, as well as the wall of the mid-gut, to pass into the blood for the general nourishment of the body.

In most animals that have attained to a high or even moderate degree of organisation there is a circulating fluid or blood which serves as the medium of exchange between the general living tissues of the body and the organs of specialised function, bringing to the tissues food and oxygen, providing the raw material for their secretions, and taking up from them waste-substances to be carried to and eliminated by the organs of excretion. As a rule these exchanges are carried on while the blood flows through vessels minutely fine with exceedingly thin walls which afford opportunity for diffusion in either direction. But in insects, as among Arthropoda generally, the blood during much of its circulatory course flows through great spaces in the body, surrounding the digestive and other organs and bathing them on all sides; thus instead of a typical body-cavity (coelom) a vast blood-space (haemocoel) occupies most of an insect's inside. From this principal cavity where food-material is absorbed through the gut-wall, the blood passes up through a perforated membrane into a special blood-space—relatively long and broad but shallow—just beneath the dorsal body-wall where the narrow tubular heart is placed, gaining entrance to the heart by means of a series of paired slits (Fig. 12, *h*). The heart's rhythmical pulsations force the blood towards the front region of the insect where it passes from the system of closed tubes into the great blood-space already described.

The elimination of nitrogenous waste-matters—among the most important end-products of the chemical changes (metabolism) always going on in a living body—is performed in insects by a set of organs highly characteristic of the class. These are elongate, narrow tubes (Fig. 10, *Mt*) which grow

out from the front end of the hind-gut and lie freely in the great blood-space that surrounds, as we have seen, the digestive system. The epithelium that forms the thin walls of these "Malpighian" tubes—so named in honour of Marcello Malpighi, the great seventeenth-century pioneer of insect anatomy—separates from the surrounding blood the waste matter in a state of solution, so that along the tubes it may pass into the intestine and out of the body.

The working of the various systems thus briefly reviewed is co-ordinated by means of the nervous system, as ever the seat of general control of an animal's activities. An insect is essentially a segmented animal, and in each segment is present a pair of closely apposed nerve-centres or ganglia, usually situated just within the ventral body-wall. The ganglia of the successive segments are linked up by a pair of longitudinal nerve-trunks, and from each ganglion nerves pass to the muscles and other structures of its segment (Figs. 10, 12), so that each ganglion, while it controls the action of organs in its own segment, is capable of receiving nerve-impulses from or sending them to other segmental ganglia. But in insects there may often be observed a tendency for the ganglia of two or more successive segments to become fused together, resulting in an integration of the nerve-centres and a consequent centralisation of nervous control. Such integration is notably illustrated by the coalescence, in all insects, of the anterior three or four ganglia of the head to form a brain (Figs. 10, *b* ; 12, *op*), situated above or in front of the mouth, and linked to the ganglia behind it by paired nerve trunks passing one on either side of the gullet. From the brain the general activities of an insect are clearly directed, yet mutilation of the creature shows that considerable power of control resides in local centres, for the hinder region of the body may, after separation from the head, continue to move in a manner seemingly purposeful.

In any animal a large number of its habitual motions may be shown to occur as definite responses to external stimulations of various kinds. Some irritable nerve-ending



receives an impression from the surroundings, resulting in the transmission of a nerve-impulse to the central system, its arrival at which may or may not result in a definite sensation, but will surely result in the transmission from the central system, to muscle-fibres or other tissue, of an impulse which will lead to suitable movement or other response—the whole operation affording an example of what physiologists call a “reflex.” In insects and other arthropods the most characteristic feature of nervous action results from the fact that, the living skin being everywhere covered by the cuticle, impressions on the nervous system can be made only through some modified part of this cuticle. Although that envelope may be generally described as a protective armour defending its wearer from outside influences, yet it possesses hundreds or thousands of admirable modifications adapted for the reception of stimuli. An insect’s body or limb-segment often bears many “hairs” or “bristles”—stiff projections, each jointed to the general cuticular surface by a flexible basal region (Fig. 1, *h*). Each hair is the secretion of a special cell of the skin, and if this cell in touch with the hair or bristle, be prolonged into a nerve-fibre running towards a ganglion, the hair is “sensory” in function, the resulting sensation being comparable to a sense such as touch, which we ourselves know by experience. Sensory hairs of this type are often especially numerous on certain appendages of the head—notably on the feelers, which are modified limbs belonging to one of the brain-segments, and on the jointed leg-like “palps” borne on some of those hinder head-limbs that serve as jaws. Even the highly specialised senses of hearing and sight depend upon specialised cuticular areas. Thin, tense patches of the cuticle in many insects are capable of being thrown into vibration by impinging sound-waves, so that adjacent nerve-endings can be affected; while in almost every insect the paired eyes, so prominent on the head, show a reticulated surface of transparent cuticular facets, each of which overlays a set of nerve-elements modified from the skin and in connection by means of the



optic ganglia and nerve-fibres with the brain. For a

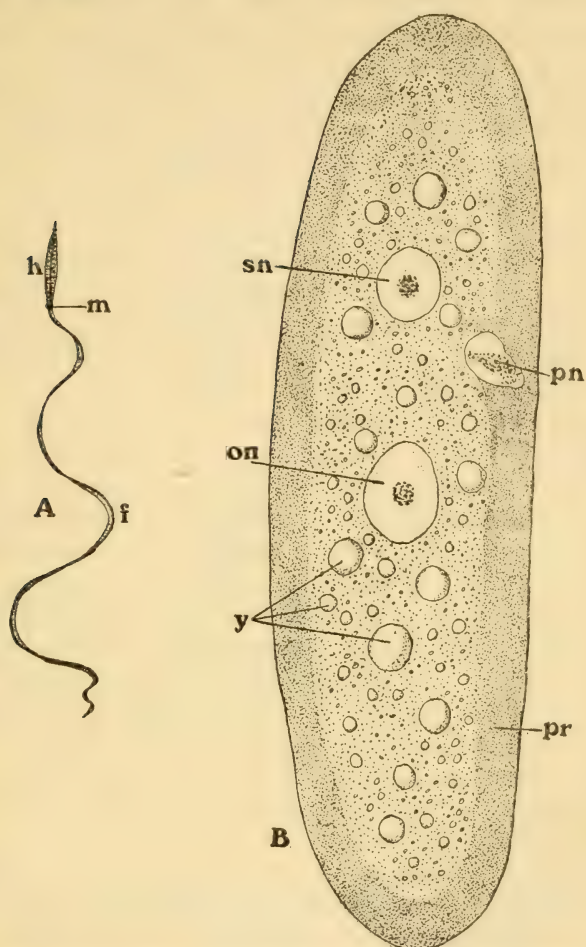


FIG. 3.—A, Spermatozoon of a Longhorn Beetle (*Morimus*): *h*, head with nucleus; *m*, middle-piece with centrosome; *f*, flagellum. B, Ovum or Egg of a Midge (*Chironomus*), *pr*, protoplasmic layer; *y*, yolk-globules; *on*, egg-nucleus; *sn*, sperm-nucleus (which has entered egg); *pn*, polar nucleus, separated from egg-nucleus.  $\times 400$ . After Ballowitz and Ritter, *Zeitschr. f. wissenschaft. Zool.* 1, 1890.

chemical stimulus to affect nerve-cells so as to give rise to sensations like smell or taste, it is necessary that the cuticle

over the receptive organ should be exceedingly thin or perforated; such sensory "pegs" or "pits" are found in large numbers on feelers and palps. Thus an insect's skeletal and protective cuticle is so modified as to ensure all needful correspondence with the outer world, while the high development of its central nervous system is correlated with behaviour often apparently intelligent.

One further aspect of the life of insects remains for discussion in this brief preliminary sketch. All animals reproduce their kind, so that any living creature that may delight us as we watch its purposeful activity reaches always its full development through a process of growth and change from simple beginnings. The details of reproduction and growth among insects are of exceptional interest to the student. The two kinds of germ-cells or gametes—the small, motile sperms and the large passive eggs (Fig. 3) are developed, as is most often the case among animals, in two sets of individuals known respectively as males and females, which often present striking difference in their outward aspect and mode of behaviour. Many male insects when compared with their females afford examples of smaller size together with more highly elaborated sense-organs, brighter colours and greater activity; it is not unusual, for example, to find flying male insects that have wingless mates, or chirping males that have silent females. The eggs of insects are relatively large with a liberal supply of food-material or yolk (Fig. 3, B, y). Fertilisation of the eggs may not follow immediately on pairing, as the sperms are received into a special female sperm-case (spermatheca) to be discharged when required as the eggs are laid. Not a few insects are derived from eggs never fertilised, providing the best known examples among animals of virgin-reproduction (parthenogenesis).

In the course of their growth, most insects undergo a remarkable process of change. The cuticle wherewith they are clothed, not being formed of living tissue, cannot grow and possesses only a limited capability of stretching; hence it must, during the insect's growth, be periodically

renewed and shed, the casting or "moult" of the exoskeleton being called an ecdysis. Often the various instars (the forms assumed by an insect in the successive stages of its life-history) differ from one another, and this is, to some degree, inevitable, since, while the vast majority of insects are winged when adult; no insect has wings when first hatched or born. The wingless young may be

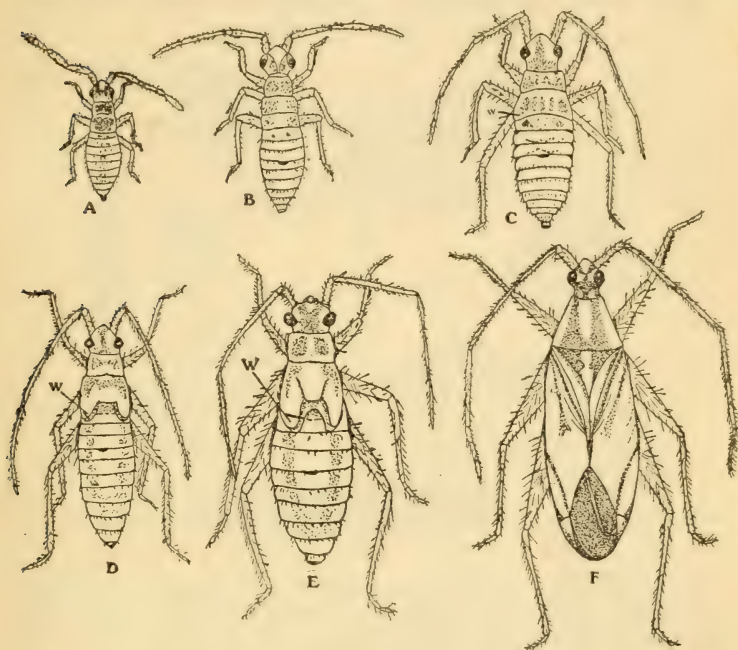


FIG. 4.—Successive instars of Meadow Plant-bug (*Leptopterna dolabrata*), Great Britain, from newly-hatched (A) to adult (F); in C, D, and E can be traced the growth of the wing-rudiments (*w*).  $\times 5$ . After A. Tullgren, 1919, and H. Osborn, *Journ. Agric. Res.* (U.S.D.A.) xv, 1918.

strikingly like the winged adult as in the case of grasshoppers and plant-bugs (Fig. 4), or to all outward seeming most unlike it, as may be seen by comparing a butterfly or moth with its caterpillar (Fig. 5), a bee with its grub, or a bluebottle fly with its maggot; in such cases the transformation exemplified in the insect's life-history is profound.



And not only is this true as regards form ; it holds frequently also as to place of abode, method of feeding, life-relations in the wide aspect. By processes of gradual growth and, at times, of apparently sudden change is the winged creature moulded to the atmosphere in and around which it lives. A crawling larva dwelling in water, breathing dissolved air and biting solid food, may be transformed into a winged aerial being, which flits or poises itself with

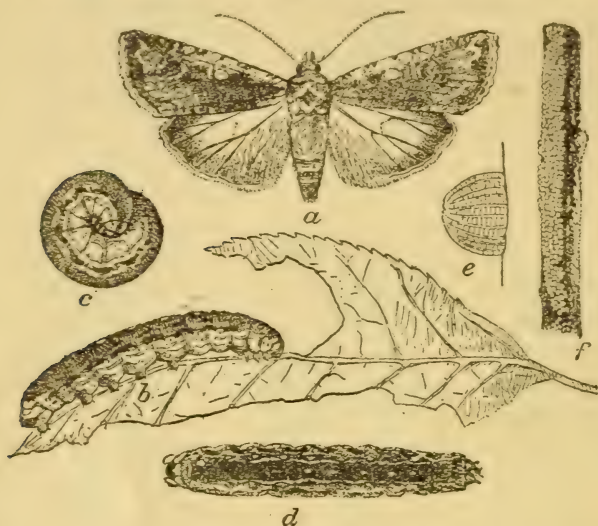


FIG. 5.—*a*, Owl Moth (*Agrotis saucia*) Great Britain ; *b*, its caterpillar, side view ; *c*, caterpillar rolled up ; *d*, caterpillar, dorsal view ; *f*, mass of eggs laid on twig. All natural size. *e*, single egg,  $\times 20$ . From F. H. Chittenden (after Howard), *Entom. Bull.* 27, U.S.D.A. 1901.

easy grace as it seeks for food in the nectar-stores of floral cups.

Among the most fascinating aspects of the study of insects must be reckoned the modes of behaviour often associated with the function of breeding. The mother lays her eggs amid suitable surroundings, often on food substances which she herself, in her winged condition, never tastes, but which supply the nutriment needed by the newly hatched grub. In some cases great care is taken



of the eggs, or the young may be fed like the helpless nestlings of birds. Thus family life of a kind is exemplified by many insects, and it is well known how, among the wasps, bees, and ants, for example, the size of the family becomes enormously increased so that the assemblage may not unsuitably be compared to a state with its "officers of sorts," and the nest to a city whose streets and habitations swarm with orderly and industrious crowds. Such "social" insects have from early times aroused the admiration of observant men who have sought to draw, for their own guidance, lessons of wisdom from the apparently intelligent behaviour of these small yet wonderfully organised fellow-creatures. Later we may have opportunity to discuss how far such comparisons between insectan and human societies may justifiably be carried.

In bringing to a close our short survey of the field which it is proposed to cover in this volume, a summary—condensed and therefore necessarily technical in mode of expression—of the main features of insect structure in relation to life-conditions may perhaps be of service.

Insects, then, are a class of the Arthropoda: segmented appendiculate animals, clothed with a chitinous cuticle which forms an exoskeleton giving attachment to striated muscle-fibres. The head, whose appendages are modified as feelers (one pair) and jaws (usually three pairs), is sharply distinct from the three-segmented thorax which bears six legs and usually four wings, the latter being dorso-lateral outgrowths of mesothorax and metathorax; thus a variety of precise and rapid motions, including flight, may be possible. The breathing-organs are complex, branching air-tubes, lined with spirally-thickened chitinous cuticle, facilitating direct gaseous exchange between tissues and atmosphere wherewith this tracheal system typically communicates through a series of paired spiracles. The digestive tube has extensive anterior and posterior tracts lined with chitin. The perivisceral and pericardial spaces are haemocoels, the latter receiving blood through its

perforated floor and transmitting blood to the heart by means of paired ostia. The organs of nitrogenous excretion are elongate, tubular outgrowths of the hind-gut. The nervous system consists of a double chain of segmentally arranged ventral ganglia with longitudinal trunks connected with an anterior complex brain. Sensory nerve-endings are affected through modified cuticular areas or outgrowths. Insects are of separate sexes (dioecious), the female producing large eggs which may, in some cases, develop parthenogenetically ; secondary sexual characters are often conspicuous. Growth is necessarily accompanied by a series of ecdyses in which a less or greater degree of metamorphosis is connected with the acquisition of wings and other structures characteristic of the adult creature.

## CHAPTER II

### FEEDING AND BREATHING

THE diverse systems of organs that build up the body of any animal and the various functions that these perform are so closely inter-related with one another, that it is impossible to consider any one system or mode of activity entirely by itself. Yet for a detailed discussion of the biology or "life-knowledge" of a creature, it is necessary to attempt, in some kind of order, a survey of its various organs and their actions, though opinions may well differ as to what order is the most convenient and reasonable. In this discussion of the Biology of Insects it is proposed to begin with the functions of feeding and breathing and the important series of changes within the body associated with these familiar manifestations of life.

All observers of nature have in mind a distinction, implied if not expressed, between living creatures and lifeless objects. In this book it is assumed that such distinction is justified, and while questions about the ultimate meaning of life must be left to the philosopher, the visible manifestations of life—the modes of behaviour of living creatures—are proper subjects of study for the naturalist. Among these, feeding is one of the most obvious, as well as one of great importance. In our introduction (p. 10 above) we have noticed that not the whole body of an insect is alive; we have dwelt, for example, on the distinction between the outer cuticle or exoskeleton, which is a horny, lifeless envelope, and the skin, a sheet of living cells beneath, by whose activity the cuticle is built up (Fig. 1).

The essential component of these cells, the substance

of the creature that is truly alive, is known as protoplasm, the "physical basis of life" as Huxley long ago called it. Protoplasm is a semi-fluid material composed of various elaborate nitrogenous chemical compounds known as proteins. These substances are of high complexity; in addition to carbon, hydrogen and oxygen, nitrogen is always present as well as a small proportion of sulphur, and a protein is now regarded as "formed by the condensation of a number of molecules of various amino-acids" (W. M. Bayliss, 1924), different combinations of these "building stones" being characteristic of different types of protein. The component molecules of protoplasm are in the colloidal state. To repair the waste which living protoplasm constantly undergoes, food in the form of protein must be obtained by the insect, and such food is found either in the tissues of plants, or in those of other insects or various animals which may serve as prey or "hosts," or in waste or decaying organic substances.

As mentioned in the introductory chapter, energy is constantly liberated in insects as in living creatures generally, becoming evident in movement and radiation of heat. The "fuel" needed to supply this energy is largely furnished by non-nitrogenous food-substances: carbohydrates such as starch and the sugars, and fats. The energy liberated in the activity of living tissues is due to the breaking down of chemically complex substances, either components or inclusions of the cell-protoplasm. The renewal or rebuilding of these requires a constant supply of food material, which must be brought to the cells in a dissolved and absorbable condition. An insect or other animal is truly fed only as the living substance of its cells is fed, and the seizing and swallowing of food, which is what many unobservant persons understand by "feeding," is really only ingestion, the necessary prelude to the true feeding process.

We may then suitably begin our study of the feeding of insects by considering some of the methods by which they procure and swallow or ingest their foodstuffs. A well-known feature characteristic of animals generally is the



possession of a digestive cavity within which the swallowed food-material undergoes the changes necessary to fit it for furnishing nourishment to the living tissues. This cavity may be regarded as a modified tube running from a forwardly situated opening, the mouth, to a hinder opening, the vent or anus, through which the useless remnants of the food are ejected. Insects, like many of the highly organised animals of various groups, have a definite head formed by the union of a number of primitive body segments, and in front of or beneath this head the mouth is situated.

An insect's mouth is furnished with jaws for seizing, masticating, piercing, sucking, or otherwise dealing with suitable food-substances. The jaws are arranged in pairs, and it was long ago shown (Savigny, 1816) that they are modified appendages belonging to the series of paired jointed limbs characteristic of Arthropods generally. These jaw-limbs differ greatly in form in different groups of insects according as they are used for biting solid food material, or for piercing and sucking or licking up various fluids. We may conveniently introduce this study of insect jaws by examining those of a somewhat primitive type of biting insect such as a common earwig (Fig. 6).

Below the face region (clypeus) of the earwig's head is hinged a median flap with straight lower edge and rounded margins. This is the upper lip (labrum) which bounds the mouth in front ; it is to be regarded as part of the insect's head skeleton (Fig. 6, A). Just behind it and only in part hidden by it, lie the front jaws or mandibles (Fig. 6, B), stout, strong organs each consisting of a single finely moulded piece, the broad base articulating with the head skeleton by means of a knob-like condyle behind and a concave surface (ginglymus) in front, the outer edge evenly rounded, trending to the sharp, inwardly directed apical teeth, the inner edge approximately straight with a ridged grinding or molar area towards its base. The two mandibles are arranged facing each other, they can be drawn together by the action of adductor or apart by abductor muscles. When the mandibles are drawn together the

apical teeth interlock and the molar areas are in contact. Thus pieces of leaves or blossoms can be seized and bitten up by the teeth, and then ground into small particles between the ridged molar surfaces which move over each other as the mandibles alternately are pulled inwards

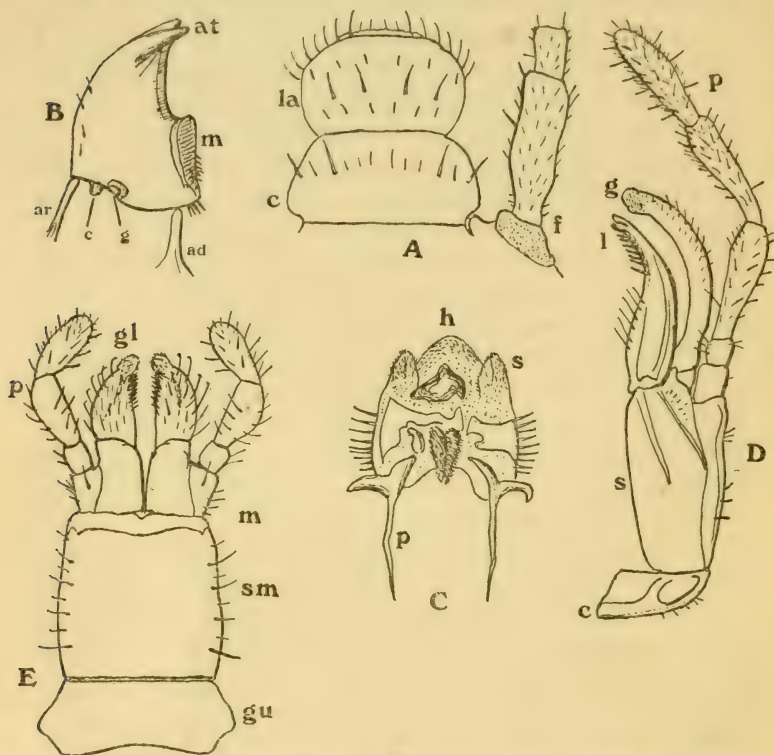


FIG. 6.—Mouth parts of Earwig (*Forficula auricularia*), A, labrum or upper lip (*la*) attached to face or clypeus (*c*), alongside base of feeler (*f*). B, left mandible (front view): *at*, apical teeth; *m*, molar (grinding) area; *c*, condyle; *g*, ginglymus; *ad*, tendon of adductor and *ar* of abductor muscles. C, hypopharynx (*h*) with superlinguae (*s*) and supporting feet (*p*). D, left maxilla (back view): *c*, cardo; *s*, stipes; *l*, lacinia; *g*, galea; *p*, palp. E, labium formed by conjoined hinder maxillae: *gu*, neck sclerite; *sm*, submentum; *m*, mentum; *gl*, united galea and lacinia; *p*, palp.  $\times 50$ .

towards the mouth by the slight contraction of their abductor muscles.

Behind the mandibles and placed farther apart from one another than they, we find a second pair of jaw-limbs, the maxillae (Fig. 6, D), which are somewhat complex in form. Each maxilla has a base composed of three pieces, two short ones arranged transversely forming a hinge (*cardo*) to which is attached a longitudinal axis (*stipes*), bearing an externally and forwardly directed jointed leg-like organ, the palp, and two lobes, of which the outer (hood or *galea*) is evenly rounded and coated with soft hairs, while the inner (blade or *lacinia*) is provided with strongish apical teeth and a row of sharp, hard spines. A live insect with such maxillae as these may be seen often to test with the tips of its palps the surface over which it walks as though to "feel" whether the material is suitable for food. The maxillary hood serves as a cover for the blade with its sharp teeth or spines, and the blades are of service in further dividing the food, already roughly masticated by the mandibles, into finer particles.

The earwig's mouth is closed behind by what is often termed its lower lip (Fig. 6, E) (*labium*). Examination of this organ soon convinces the student that it is composed of a pair of maxilla-like limbs joined together by their bases, for paired blades, hoods and palps, though smaller than their counterparts of the maxillae, are evident, and the basal plates (*mentum* and *submentum*) of the *labium* can readily be compared with the fused hinges and axes of the maxillae.

Situated between the two maxillae in the middle of the mouth is the tongue or *hypopharynx* (Fig. 6, C), a comparatively soft and membranous organ, yet covered by cuticle beset with closely arranged hairs at the top, supported by a pair of strong chitinous basal pieces, and having a pair of bristly lobes (*superlinguae* or *paragnaths*) attached to its front face. Behind it—that is to say between it and the *labium*—opens the duct of the salivary glands, to be described later. The hairy tip of the tongue may be regarded as concerned with the appreciation of food taken into the mouth.

Such jaws as these are adapted for seizing and masticating solid food which is passed on into the digestive canal

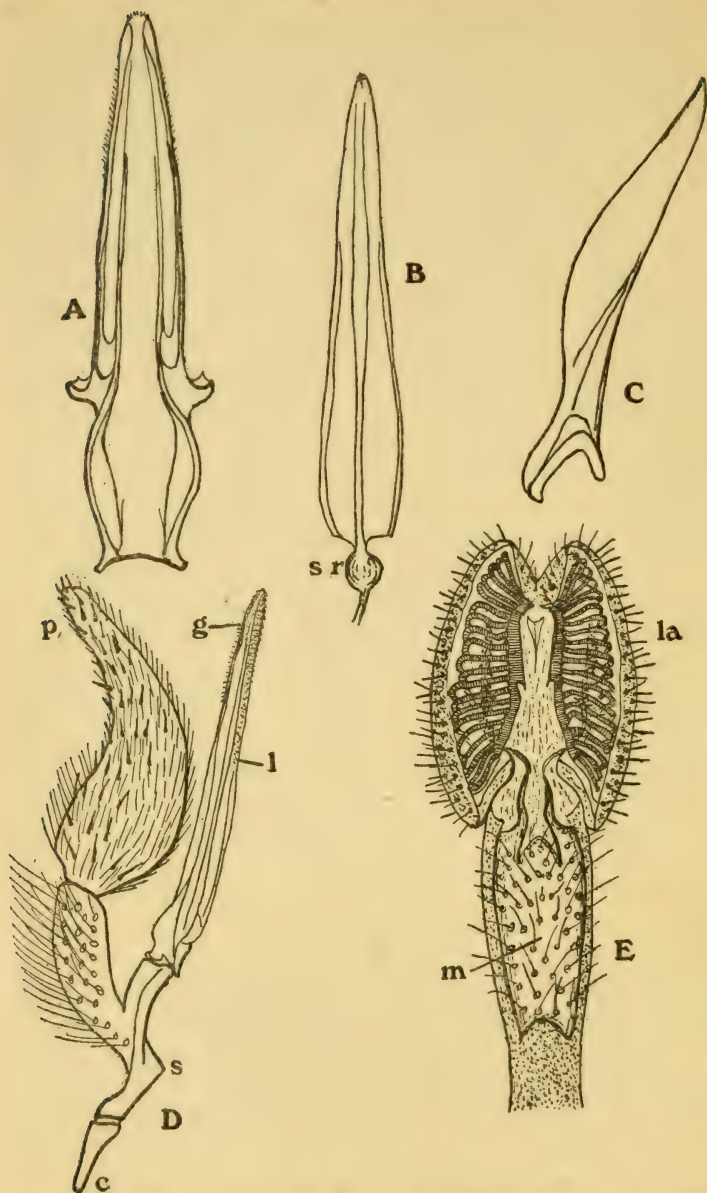


FIG. 7.—Mouth-parts of Breeze-fly (*Theriopectes*). A, labrum-epipharynx. B, hypopharynx (*sr*, salivary reservoir); C, mandible. D, maxilla (*c*, cardo; *s*, stipes; *l*, lacinia; *g*, galea; *p*, palp). E, labium (*la*, labella with pseudotracheal channels for suction; *m*, mentum).  
 × 30.



in small lumps. Very different is the form of the jaws of insects that take their food in the liquid state. As an example we may consider a blood-sucking fly (Fig. 7) such as a breeze-fly (Tabanid). Here the median (unpaired) organs of the mouth—the labrum-epipharynx, and hypopharynx—are formidable dagger-like piercers (A, B) projecting downwards from the head. The mandibles (C) are curved, with the base broad, the sharp edges tapering to a fine point, like the blade of a broadsword; by the action of muscles these can be thrust out or pulled back. The maxillae (D) are straight, narrower than the mandibles, with their tips not only sharply pointed but armed with formidable barbs so that when thrust into the skin of the animal whose blood is being sucked they hold firmly. Each maxilla appears to be composed of lacinia and galea closely united along their whole length. There is a short hairy palp (Fig. 7, D, *p*) consisting of a single elongate segment broad at the base and tapering to a point. The labium (E) is a thick leathery organ with conspicuous bi-lobed extremity along which run numerous channels strengthened by chitinous transverse rings, through which the blood is drawn into the hollow base of the labium, whose cavity leads onward to the mouth and gullet. Other insects that feed by suction may differ from the breeze-fly in the form and arrangement of their jaws and other mouth parts. Among bugs (Fig. 8) and their relations, such as “greenfly” for example, the labium is modified into a stiff jointed “beak” (rostrum) with a groove extending along its front aspect. Over the base of this groove lies the short, acute, flexible labrum, and within are found the mandibles and maxillae, slender, strong piercers, the tips of the former being barbed like those of the breeze-fly (Fig. 8, *Mn*, *Ma*). These piercers can be thrust out beyond the extremity of the beak, so as to puncture the tissues of a plant whence sap can be sucked, or of an animal whence blood or other nutritious fluid can be drawn. Such liquid food is sucked in through the exceedingly fine tubular channel (Fig. 8, B, *sc*) formed by the concave inner surfaces of the piercers, and

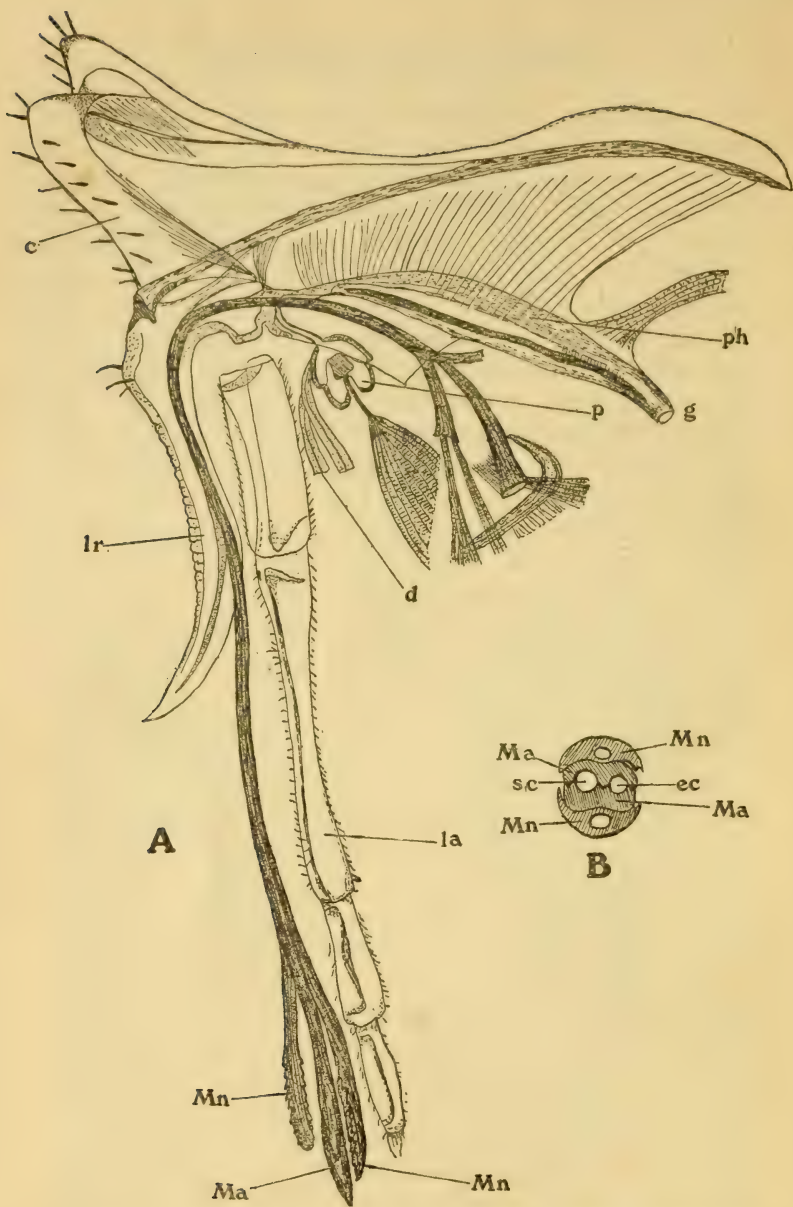


FIG. 8.—A, Jaws and mouth of Shield-bug (*Tessaratomia*) shown as dissected from the side with the labium (*la*) displaced backwards.  $\times 22$ . B, Cross-section through piercing stylets of a shield-bug (*Graphosoma*).  $\times 300$ . *Mn*, mandible; *Ma*, maxilla; *c*, clypeus; *lr*, labrum; *ph*, pharynx; *g*, gullet; *p*, salivary pump with muscle; *d*, salivary duct; *sc*, suction canal, and *ec*, excretory canal between maxillae. After C. Bugnion, *Arch. Zool. Exp.* (5) vii, 1911.

past the bases of these it is passed on into the mouth and gullet.

Many sucking insects, however, depend upon liquids that can be reached without the necessity of piercing any plant or animal tissue. A common house-fly belongs to the same order as the breeze-fly just mentioned, and observant persons must notice how that familiar insect wanders over lumps of sugar in a bowl, applying to their surface the thickened tip of a leathery proboscis which appears to be hinged on beneath the head. This is a labium, corresponding closely with that of the breeze-fly, but with the bi-lobed tip (labella) broader, more elaborately formed and with more numerous channels. The house-fly has no mandibles and its maxillae are represented only by their basal regions and their palps; the insect sucks its food on exposed surfaces of many kinds.

Another type of sucking insect whose mode of feeding may often be observed is a butterfly or moth. Such a graceful creature is seen to rest on a flower-head or poise itself in front of a blossom, and unroll a delicate flexible "trunk," which when not in use rests coiled up in a spiral beneath the head and between the prominent scaly labial palps. This trunk (Fig. 9) is composed of the elongate hoods or galeae of the maxillae, which, being grooved on their inner aspects, are modified into flexible half-pipes, provided with interlocking hooks or spines so that the pair of organs can be conjoined to form a tubular sucker whose tip can be stretched out to reach the nectar at the bases of the floral leaves. The butterfly's maxilla has no blade (lacinia) and its palp is reduced to a tiny scale-bearing process, while the mandibles are altogether wanting or represented only by minute vestiges.

Thus, by means of the jaw-limbs and other feeding structures, variously modified, as has been seen, in different insects, the food is passed into the mouth and thence into the gullet or front region of the digestive tract (Fig. 10, *oe*). This, as well as the succeeding regions—the crop (*cr*) and the proventriculus (*pv*)—is derived from the fore-gut, an

inpushing of the skin at the mouth-region and consequently lined with a chitinous layer which is an extension of the outer cuticle. The details of structure of the gullet and

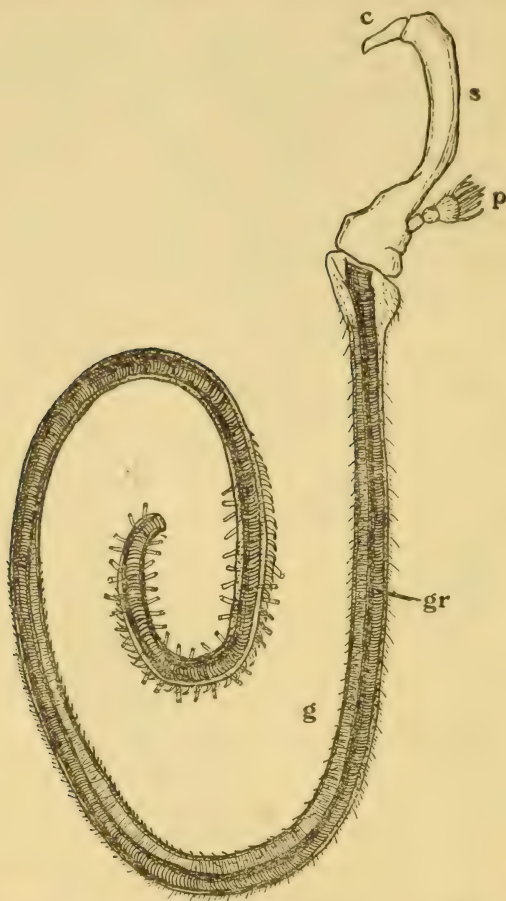


FIG. 9.—Maxilla of an Owl Moth (*Agrotis*). *c*, cardo; *s*, stipes; *p*, palp (vestigial); *g*, long flexible galea with groove (*gr*) on its inner face and coupling hooks and sensory organs towards its tip.  $\times 50$ .

crop differ—like those of the jaws—in insects that differ in the nature of their food. Thus in a cockroach, earwig, or beetle, which swallows smaller or larger solid lumps, the



narrow tubular gullet traverses the thorax and then, in the abdomen, opens out into a capacious ovoid crop in which a quantity of material can be stored awaiting digestion. In the bee the crop is similar in form and arrangement but relatively smaller (Fig. 10, *cr.*). A butterfly has the front end of the gullet expanded into a small spherical bulb situated in the head, this by the alternate expansion and contraction of its wall, induced by the action of suitably arranged muscles, sucks liquid nectar into its cavity and then propels it along the gullet into the crop. And the butterfly's crop is not simply an expanded region in the course of the fore-gut, it is a sub-globular sac forming a lateral outgrowth at the hinder end of the gullet, so that the liquid food may accumulate in it, and pass on later to the further regions of the digestive tube. In a two-winged fly of the common housefly or bluebottle type, the gullet is prolonged backwards far beyond the front end of the abdomen, widening into the sub-globular or ovoid crop which, having no other outlet, serves in this case also as a reservoir for liquid food.

The proventriculus (Fig. 10, *pv*) is the third or final section of the fore-gut. In a biting insect such as a cockroach or beetle, this forms a short region of the digestive tract, sub-globular or hemispherical in shape, with the muscular coat of its wall very thick, and its internal chitinous lining raised into strong tooth-like ridges which project into the cavity. Contraction of the muscle fibres tends to bring these teeth together in the mid-cavity of the organ which is frequently spoken of as a "gizzard," under the assumption that its function is the crushing of solid food-material. Probably, however, the action of the proventriculus is rather that of a strainer, preventing the passage of the food into the middle region of the food-canal until its treatment in the fore-gut has been brought to completion. In very many insects the hindmost region of the proventriculus projects as a comparatively narrow tube into the front end of the stomach or mid-gut. This arrangement may be well seen in that familiar insect the hive-bee (Figs. 10, 11),

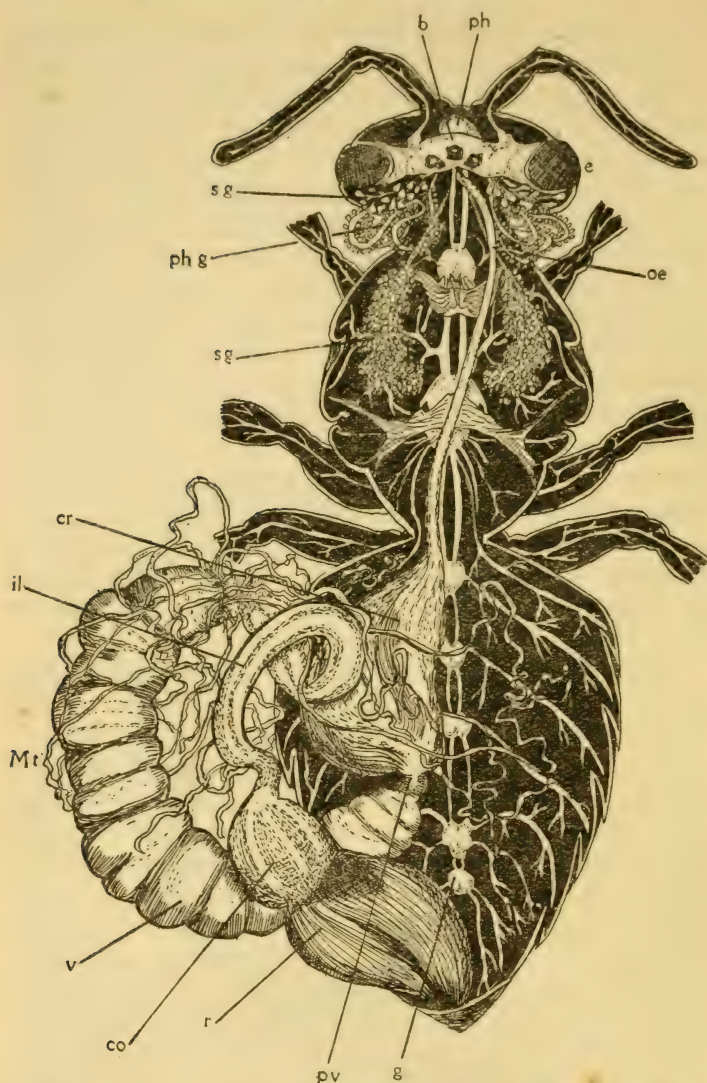


FIG. 10.—Dorsal Dissection of Worker Honey Bee (*Apis mellifica*), showing Digestive and Nervous Systems. *ph*, pharynx; *oe*, gullet; *cr*, crop or "honey-stomach"; *pv*, proventriculus; *v*, ventriculus or chyle-stomach (mid-gut); *il*, ileum; *co*, colon; *sg*, salivary glands; *phg*, pharyngeal glands; *Mt*, Malpighian tubes; (chyle stomach and intestines are displaced to left to expose the nerve-cords connecting the chain of ganglia (*g*); *b*, brain, the three simple eyes (ocelli) above it; *e*, compound eye.  $\times 10$ . Adapted from R. E. Snodgrass, *Anatomy of Honey Bee* (U.S.D.A.) 1910.

and a study of the working of the parts of this region of the food-canal shows clearly that the proventriculus acts as a strainer ; it was long ago named the " honey-stopper " by the various writers on the anatomy of the hive-bee. Here the organ is quadrate in cross-section, lined with four prominent chitinous ridges which are separated by the contraction of longitudinal muscles or approximated by the contraction of circularly arranged fibres. This quadrate " stomach-mouth " can be seen to close and open rhythmically when the digestive tube is slit up in a freshly killed bee. Pollen-grains are thus allowed to pass on into the stomach, the chitinous lining of the proventriculus bearing hair-like, backwardly directed outgrowths which prevent the return of solid particles into the crop. The liquid nectar or honey can, however, be forced in either direction, as the need for digestion, absorption, or storage may require.

While in the crop, the food is mixed with saliva or spittle, secreted by the insect's salivary glands (Fig. 10, *sg*), which lie on either side of the gullet and open by special tubes or ducts into the median tube which enters the mouth between the tongue and the labium. It is noteworthy that the salivary ducts, being outgrowths of the fore-gut, have a chitinous lining which is often spirally thickened as in an air tube. The cells of the glands contain large bent elongated bodies, the secretory capsules, which may be nuclear in their nature. The saliva is an alkaline fluid containing a diastatic ferment which acts on carbohydrate food materials. A reservoir for storing saliva between feeding-times is usually associated with these glands, which are very much larger in plant-eaters than in insects of prey. In bees they are remarkably numerous and complex, and their secretion is partly effective in transforming the nectar sucked from blossoms into honey, the cane sugar (sucrose) of the former being " inverted " to levulose and glucose. But this action is mainly due to ferments or enzymes (sucrase) present in the gastric juice, which, formed in the middle gut or stomach, is passed forward into the crop. The nectar sucked by bees from flowers is stored in the crop, which is



therefore often termed the "honey-stomach," and after undergoing the digestive process therein, is regurgitated as honey for use in feeding the inmates of the hive or for deposit in the waxen chambers of the comb.

From the proventriculus an insect's food passes on into

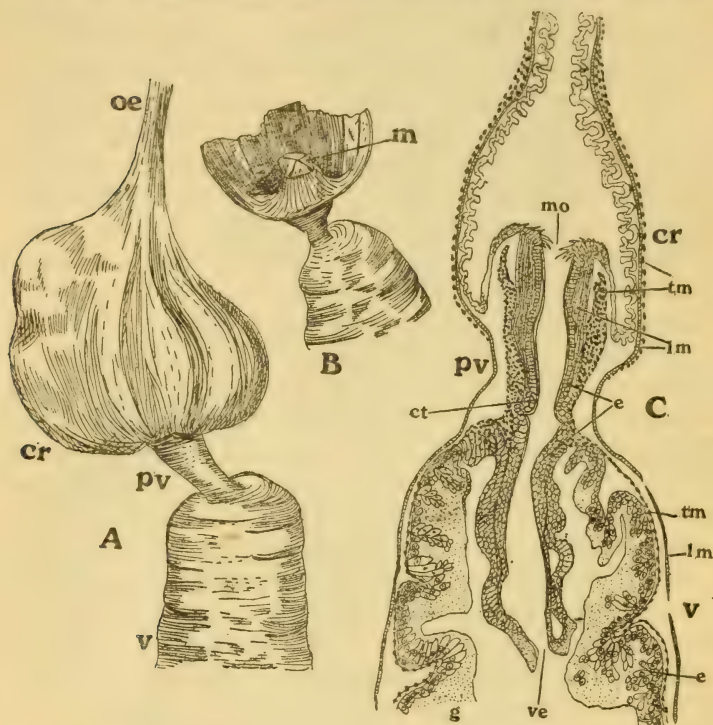


FIG. 11.—A, Crop (*cr*), proventriculus (*pv*), and chyle-stomach (*v*) of Honey Bee worker (*Apis mellifica*). B, The same with most of the crop-wall removed to expose "stomach-mouth" (*m*).  $\times 10$ . C, Longitudinal section through the same organs of a queen bee: *mo*, stomach-mouth; *ve*, proventricular valve; *lm*, *tm*, longitudinal and transverse muscle-layers; *e*, epithelium; *ct*, cuticular lining; *g*, gelatinous secretion whence peritrophic membrane is formed.  $\times 40$ . After Snodgrass.

the stomach (ventriculus or mid-gut (Figs. 10, 11, *v*), usually cylindrical in form. This is lined by a sheet of columnar cells, which may have their free surfaces thickened to form an intima, or the cells may project as fine processes



into the cavity of the organ, but they never secrete a chitinous cuticle. This sheet of cells (or epithelium) is often thrown into ridges or prominences that project on the free, inner surface of the stomach, with intervening furrows or depressions (Fig. 11). Outside is a comparatively thin muscular coat, the rhythmic contraction of whose fibres works the contained food-mass through the organ. At the front end of the stomach there are usually blind outgrowths—the pyloric caeca—which in different insects assume the form of elongate tubes or of comparatively short pouches. The cells which line these tubes or pouches—formed of necessity as an extension of the stomach epithelium—secrete the gastric juice which, besides diastatic ferments, contains a proteoclastic ferment whose function is to act on the protein constituents of the food. Gastric juice may also be formed in the pits or depressions already mentioned as often numerous on the lining of the stomach.

In many insects the food contents of the stomach are not in direct contact with its wall. They form a rod-like mass traversing the stomach from end to end, and surrounded by a delicate coat—the peritrophic membrane. The stomach contents of insects are alkaline, their reaction thus offering a contrast to the acid nature of the stomach contents of a vertebrate animal, and suggesting that the insectan gastric juice is analogous to the pancreatic rather than to the gastric juice of a vertebrate.

The lining cells of the stomach that are glandular in function, liberate their secretion into the cavity of the organ. The secretion is usually a fluid poured out over the general surface of the epithelium; but in certain fly-larvae and other insects A. van Gehuchten (1890) and other investigators have shown that small bladder-like processes grow out from the stomach cells and become constricted off so as to float freely in the cavity; these can convey the digestive juice to the central mass. F. W. Cragg has shown (1920) that the cells lining the stomach of blood-sucking breeze-flies (*Tabanus*) throw off their secretion as a mass of globules which become broken up. As the secreting cells wear out

they are replaced by basal cells which grow towards the surface and regenerate the lining layer. In the stomach cavity of bees a large number of small spherical clear, cell-like bodies can be distinguished, as Snodgrass (1910) and other observers have described; these have a similar origin and function. The peritrophic membrane is believed to be formed in many insects by the envelopes of such cells, thrown off by the epithelium; but in other cases it appears to be due to a secretion (Fig. 11, g) formed in successive layers by the cells of the stomach, as described by R. E. Snodgrass (1925) for the Honey Bee.

Brought thus into close touch with the central food-mass, the digestive juice mixes with the nutrient substances and the proteoclastic ferment acts on the proteins, breaking them up into their constituent amino-acids. In many plant-eating insects it has been shown that diastatic ferments in the juice act on the starch of the food converting it finally into a sugar (monosaccharide) with a relatively small molecule. In the stomach also it appears that fatty constituents of the food of many insects are emulsified, at least in part, and hydrolysed by the action of special (lipoclastic) enzymes, giving rise to glycerol and fatty acids. Thus the various nutrient substances are reduced as regards the complexity of their chemical composition and prepared for absorption in the soluble state by the living cells that build up the insect's organs and tissues. This, as has already been emphasised (p. 16), must be regarded as the true feeding process. Absorption of the digested food-substances is carried on through the wall of the stomach. H. Jordan (1913) proved that various insects, with whose food iron-compounds had been mixed, showed the presence of iron in certain cells of the stomach epithelium. The comparative thinness of the stomach-wall would suggest that there absorption must be actively carried on. But there seems no doubt that in the terminal region of the food-canal—the hind-gut as it is called—absorption also takes place.

The hind-gut or intestine of an insect has, like the fore-

gut, its inner sheet of cells formed by inpushing of the outer skin, and therefore lined with a chitinous sheet that is an extension of the cuticle. The hind-gut is readily divisible into several regions. The front portion is usually a cylindrical tube of narrower diameter than the stomach, and a section immediately behind the stomach may be distinguished—in a bee (Fig. 10, *il*), for example—as a small intestine or ileum. From the extreme front end of this are given off the elongate Malpighian or excretory tubes (Fig. 10, *Mt*), already briefly mentioned (p. 7), whose form and function will be discussed more fully later (pp. 38–39). The food-canal widens behind into the large intestine or colon (*co*). In these regions the cellular layer (epithelium) is regular and distinct, its inner surface protected by a delicate but definite chitinous lining, while the muscular coat is relatively thick, the contractions of its circularly arranged fibres driving on the contained food still undergoing digestion. The terminal portion of the hind-gut is the rectum, usually a capacious, bladder-like organ (Fig. 10, *r*) with relatively thin walls, often thrown into longitudinal folds that form ridges and furrows. Here the epithelial layer is largely degenerate, the cell boundaries being indistinct except in certain regularly arranged blind tubes or pouches—the so-called rectal glands—whose lining cells are large and columnar. The secretion of these glands is apparently not digestive but auxiliary to the ejection of the unusable residue of the food.

Despite the cuticular lining of the hind-gut there seems to be no doubt that food-absorption takes place through its walls. S. Metalnikoff (1896) states that the cuticle of the cockroach's large intestine is porous and that the epithelium cells absorb particles of iron administered in the insect's food. In hive-bees the rectum often contains a quantity of pollen-grains, which constitute the source of the nitrogenous and fatty food-supply of these insects; only on reaching the rectum is the digestion of much of the pollen concluded, so the high probability of the absorption of the digestive products there may be inferred.



The rectum opens at the vent (or anus) on the hindmost segment of the insect's abdomen ; through this the rejected remains of the ingested foodstuffs are passed out. The nature of this excrement varies necessarily with the insect's diet. Its aspect often proclaims the kind of solid food-materials that have been devoured ; the little pellets passed by a leaf-eating caterpillar are green and show the microscopical characters of leaf-tissue, while the " frass " ejected by a wood-eating larva has the aspect of fine sawdust. Curious and interesting is the fact that the liquid excrement of such sucking insects as greenfly, still containing a proportion of available carbohydrate, serves as an acceptable food to many kinds of ants which follow and tend the aphids in order to obtain it. Many insects while in the larval state pass no excrement from the food-canal. In the " ant-lion " grubs of lace-wing flies the vent is closed, while in the grubs of wasps, bees, and ants there is no outlet from the stomach into the hind-gut until the close of larval life. On the other hand, there are many insects—for example mayflies, silk-moths, and botflies—which in the adult condition take no food at all. Their jaws are reduced and useless and their mouths closed, but the various regions of their food-canals are developed like those of their relations that feed until the end of their lives. The consideration of details as to the immense variety of methods of feeding among insects must, however, be postponed until later chapters dealing with their general habits and mode of life.

We have seen that the digested and mostly soluble food-constituents are absorbed by the living cells that form the epithelial lining of the food-canal. Thence they are conveyed to all other tissues of the body in the circulating fluid well known as the blood. The blood and the circulatory system therefore next demand our attention.

In most insects the blood is colourless, consisting of a watery plasma with salts, sugar, proteins, and amino-acids in solution, in which float small cells with distinct nuclei and often a tendency to change periodically their shape,



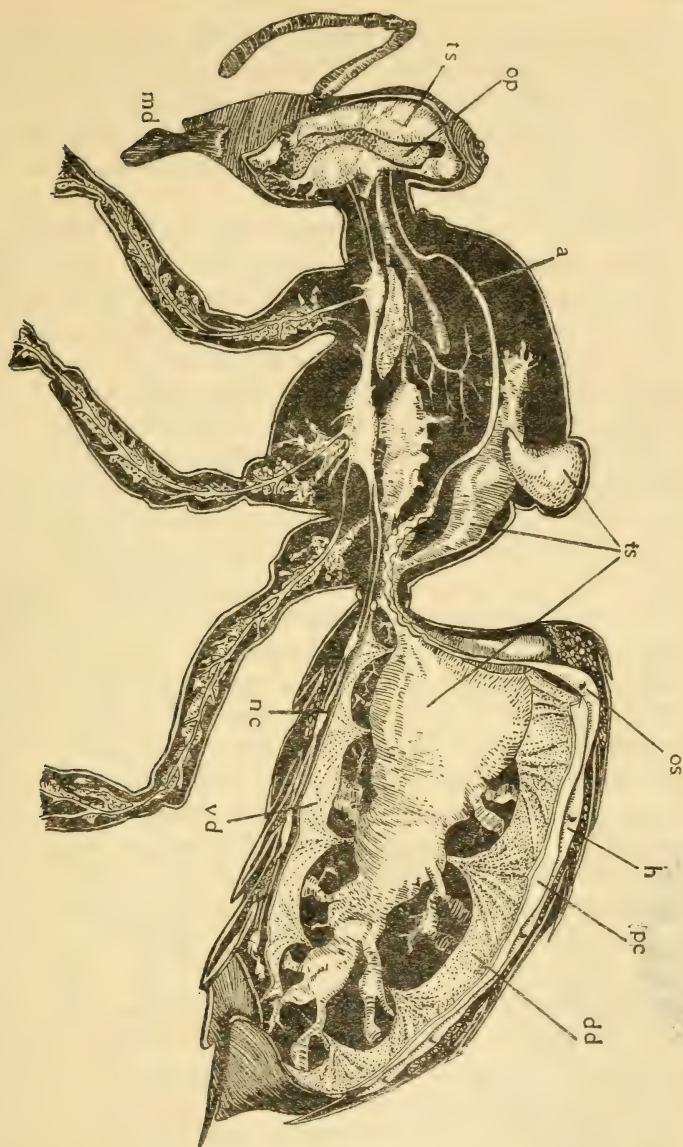


FIG. 12.—Lateral Dissection of Worker Honey Bee (*Apis mellifica*), showing Nerve-cord (*nc*) and Circulatory and Respiratory Systems. *ts*, tracheal sacs connected with air-tubes. *h*, heart, with its paired slits (ostia) *os*, surrounded by pericardial blood-space (*pc*); *dd*, dorsal and *vd*, ventral diaphragms; *a*, aorta; *op*, optic lobe of brain; *md*, mandible.  $\times 10$ . After R. E. Snodgrass, 1910.

resembling thus the leucocytes or "white corpuscles" of the blood of vertebrates. When, as is sometimes the case, an insect's blood is coloured yellow, green, or even red, the pigment is dissolved in the plasma, not, as in the red blood of vertebrates, concentrated in the specialised cells known as "coloured corpuscles."

The blood, being the circulatory agent in the body, must be kept moving in a constant and regular flow. The propellant organ for this circulation is the heart (Fig. 12, *h*), which has already (p. 6) been briefly described as a narrow tube running fore and aft in the middle axis of the insect, just beneath the dorsal body-wall, while below it a delicate membrane is stretched from side to side, forming the floor of the shallow pericardial chamber (Fig. 12, *pc*) in which the heart lies. It will be remembered that this pericardial cavity is a blood-space. The heart is formed of a variable number of chambers arranged one behind the other in a series, agreeing more or less with the segmentation or serial repetition of similar parts that characterises the body of an insect or other arthropod. But while in a cockroach the heart extends the whole length of the body, with thirteen chambers corresponding to the three thoracic and ten abdominal segments of the insect, in a bee there are only four chambers all situated in the abdomen, while in a few insect types only a single chamber can be recognised. The wall of the heart is muscular, its hinder end is closed and the blood driven through the successive chambers towards the head, the wave of muscular contraction passing on along the tube from behind forwards. Each chamber is somewhat wider at its hinder than at its front end, where the constricted portion is provided with a valve that allows the blood to flow forward but not to return towards the tail. Into the hinder widened end of each chamber open a pair of minute slits (*ostia*) provided with valves which allow the blood to pass into the heart from the surrounding pericardial blood-space, but not in the reverse direction. As, therefore, the rhythmic contractions of the tubular heart drive the blood constantly forward towards the head, a

steady flow passes into each chamber of the heart from either side of the shallow blood-space in which it lies.

The front end of the heart passes into a narrow median tube, the aorta or main artery of the body (Fig. 12, *a*). Thus there is beneath the dorsal wall of an insect, a continuous longitudinal blood-vessel, of which the hinder region is heart and the front portion aorta. The relative lengths of these two portions differ in different insects; from what has already been stated it may be realised that while in a cockroach the aorta begins at the front end of the thorax, in a bee it begins towards the front end of the abdomen. Through the aorta therefore the blood is propelled forwards into the head. Now, in back-boned animals it is well known that the blood passes from the aorta into a well-developed system of branching arteries and then circulates through a network of minute vessels, the capillaries (through whose excessively thin walls exchange of substances can go on with the fluid lymph that bathes the tissues), and is returned to the heart by a set of veins. But in insects there is no such "closed" circulatory system. Here the blood streams out from the open front end of the aorta, bathes the brain, passes backwards through the thorax surrounding the large muscles that move the legs and wings, and flows into the abdomen, whose cavity has already been defined as a great blood-space surrounding the digestive tube. In many insects there is in the abdomen a definite ventral blood-space, in which the nerve cord lies; this space is roofed by a delicate diaphragm whose contractions drive the blood upwards into the main cavity of the body. This cavity having the ventral diaphragm just mentioned as its floor, is roofed by the thin membrane already described as the floor of the pericardial space. Into this latter the blood streams from the large main cavity below, passing in some insects—cockroaches, for example—through minute holes or pores in the membrane, in others—such as beetles and bees—around the segmentally scalloped edges of the membrane. From the pericardial space, as already mentioned, the blood flows back into the



heart through the paired slits in its wall, and thus the course of the circulation is complete.

In insects, as in the whole great group of the Arthropoda, the blood, streaming through the spacious cavities of the body, comes into direct contact with the tissues. Thus the absorbed products of digestion can diffuse through the wall of the stomach and intestine, so as to pass in solution into the blood. And as the blood directly bathes all the living tissues of the body it supplies continually to the cells whether of muscle or nerve, gland or skin, germ or tube-wall—the materials which they need for building up the complex proteins that compose their living protoplasm, and the fuel that is required for the support of combustion and the liberation of energy. There is reason to believe, from analogy with what is now known to occur in vertebrates (Bayliss, 1924) that the proteins of the cell are built up of the amino-acids carried in the blood, so that in the economy of the living body the analytic action of the digestive organs is succeeded by a synthesis of protein.

The carbohydrate "fuel-food" is absorbed by the intestinal wall, circulates in the blood, and is supplied to the tissues in the form of monosaccharide. Insects have no special organ comparable to the liver of vertebrates and molluscs in which the monosaccharide sugar is transformed into polysaccharide glycogen and so stored up, to be drawn on as required and reconverted into sugar circulating in the blood. But in many insects glycogen probably forms a carbohydrate store, and this may especially be expected to occur in larvae preparing for the great expenditure of energy involved in transformation. J. Straus has shown (1911) that nearly a third by weight of the substance of bee-grubs after dessication consists of glycogen. Stored in the cells of the fat-body, the glycogen is utilised for the reconstruction of tissue that marks the pupal period during which it is retransformed into sugar and disappears.

Fat is absorbed in the form of an emulsion or dissociated into its component acid and glycerol, to be afterwards re-synthesised so that the minute fat-globules are passed



into the blood, and serve along with the carbohydrates as "fuel-food." In very many insects comparatively large masses of fatty tissue lie around the food canal in the great blood-space, or on either side of the heart in the pericardial wall. Such a "fat-body" may reasonably be regarded as a reserve of lipid food-material on which the organism can draw for the needs of its life-activities. The fat-body of a mature larva is often relatively enormous, in view of the coming transformation. Besides fat-globules the cells of an insect "fat-body" contain protein granules, that serve as a store of nitrogenous food. It has been shown by G. A. Koschevnikov (1900) and others, by means of experiments on larvae provided with coloured foodstuffs, that the store of fat may be elaborated from nitrogenous food as well as from the sugar (carbohydrate) present in honey. Thus while much of the material on which an insect feeds goes rapidly to repair its constantly wasting living substance, or to supply the energy needed for its activities, much is stored in forms convenient for future utilisation.

The transformations of energy that continually go on in the insect's tissue depend therefore on chemical reactions between the cells themselves. The contraction of muscle fibres, and the more delicate and obscure physical changes concerned in the production of the nerve-impulses to be discussed in some detail in our next two chapters, are due to the liberation of energy resulting from chemical dissociation. It has been seen how these cells are supplied by the blood with the necessary materials for building protoplasm and with a constant stream of readily available fuel. These supplies themselves depend on the digestive processes carried on in the food-canal and due to the action of the digestive ferments or enzymes on the ingested food-substances. The formation of the digestive juices is the work of the cells of the salivary and gastric glands. These cells are, like all other cells of the body, dependent for their "raw material" on the substances supplied to them by the blood, whence each gland extracts constituents which it needs, and elaborates them into its own appropriate secretion.

We are compelled to regard every cell—whatever be its specific function—as a minute but marvellous laboratory in which the characteristic chemical changes are continually wrought through the influence of unknown ferments formed within the cell, “intracellular enzymes” as they have appropriately been called.

The chemical processes thus briefly reviewed are necessarily accompanied by the production of waste substances which must be eliminated from the body ; thus we are led to consider the subject of excretion. The proteins of the

living tissue, continually built up from the materials supplied in the blood, are continually broken down through the activities of the cells, and thus nitrogenous waste-products—of simple chemical composition when compared with the immensely complex proteins—are set free. Just as the blood resigns to the tissue-cells the needed food-materials, so it takes from them the effete waste-substances, carrying these to

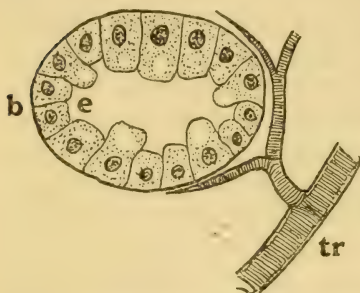


FIG. 13.—Malpighian Tube of Honey Bee (*Apis mellifica*) shown in oblique cross-section. *e*, epithelium ; *b*, basement membrane ; *tr*, small tracheal tube with fine branches on surface of Malpighian tube.  $\times 450$ .

those organs of excretion whose function it is to eliminate them from the body.

In most of the great groups of animals the organs of nitrogenous excretion are essentially tubular in structure, consisting of tubes or groups of tubules around whose walls blood may circulate—whether flowing through capillary vessels or freely bathing the cells—and into whose cavities the waste products may be passed, as the tubular excretory systems lead directly or indirectly to some outward opening of the body. In insects, as has already been mentioned, the organs of nitrogenous excretion are the Malpighian or kidney-tubes (Fig. 10, *Mt*) which grow out from the front

ends of the hind-gut into the great blood-space. When a tube is examined microscopically its wall (Fig. 13) is seen to be composed of a single layer of glandular cells with a thin basement membrane surrounded in some insects—as shown by L. Léger and A. Dusboscq (1899) and by L. Eastham (1925)—by delicate muscular fibres, which by their contraction may assist the passage of the excretion towards the intestine. The tubes lie freely in the great blood-space, floating as it were in the blood currents and capable themselves of bending and extending movements. Chemical examination shows that the tubes contain such compounds as oxalates and urates besides amino-acids such as leucin. These substances—resulting from the disintegration of protein or due to excess of nutrient materials in the blood—are extracted from the blood by the cells of the tubules or elaborated by these cells from other related substances held by the blood in solution. An interesting feature in these excretory tubes of insects is the variation in their number. Moths and butterflies have but two, beetles four or six, produced apparently by a branching of the original pair, while cockroaches, grasshoppers, bees and wasps have a large number, in some cases over a hundred, also derived by elaboration from the simpler condition. In various insect larvae as well as in some wingless springtails, the fat-body may contain concretions of urates, the waste material being thus segregated and stored, but not actually removed from the body.

More than once it has been pointed out that the liberation of energy required for the performance of an animal's activities is connected with a combustion process constantly going on in the tissues. For the support of this combustion a supply of oxygen is necessary, while the products of combustion—water-vapour and carbon dioxide—must be eliminated from the body. This important work is the function of the breathing organs or respiratory system. The remarkably characteristic form and mode of action of the breathing organs in insects have already (pp. 4-5) been very briefly described. In the vast majority of animals the



blood acts as a carrier of oxygen to the tissues and of combustion-products from them, fresh oxygen being obtained and the waste water vapour and carbon dioxide given up, as the blood passes through the fine vessels or passages of the breathing organs, such as the lungs of terrestrial and aerial creatures, or the gills of aquatic animals that are dependent for their oxygen-supply on the air dissolved in the surrounding water.

In all typical insects breathing is carried on by means of a set of branching air-tubes, a tracheal system; the fine, thin-walled terminal branchlets lead into minute tracheoles whose delicate walls are in closest contact with the various organs and tissues of the body. Thus gaseous exchange is effected directly between the insect's living substance and the air contained in the tracheoles, the oxygen passing in from the atmosphere and the carbon dioxide and water vapour passing out to it by means of a set of diffusion processes accompanying alternate intakes and expulsions of air. The air-tubes of an insect (Fig. 13, *tr*) are, as already mentioned, due to ingrowths of the skin, and are naturally therefore lined with an extension of the chitinous cuticle. It is surely suggestive that the oxygen of the free air which surrounds the insect's body should be brought into touch with the creature's inner tissues by a series of actual ingrowths of the skin with its overlying cuticle, each ingrowth dividing and branching repeatedly, pushing thus its way ever more deeply among the masses of living cells which vary greatly in form and function but are all alike hungry for oxygen.

For the greater part of their course an insect's air-tubes have their chitinous lining thickened spirally, so that when broken the wall of the tube shows the appearance of a partially unwound thread (Fig. 13, *tr*). Below the firm lining is the epithelium or cellular layer which is the continuation of the skin; outside this is a thin, supporting "basement membrane." The spirally thickened chitinous lining of the air-tube has an important bearing on the function of breathing. It gives such firmness to the tube-wall that this cannot collapse, yet it yields to some extent to the pressure



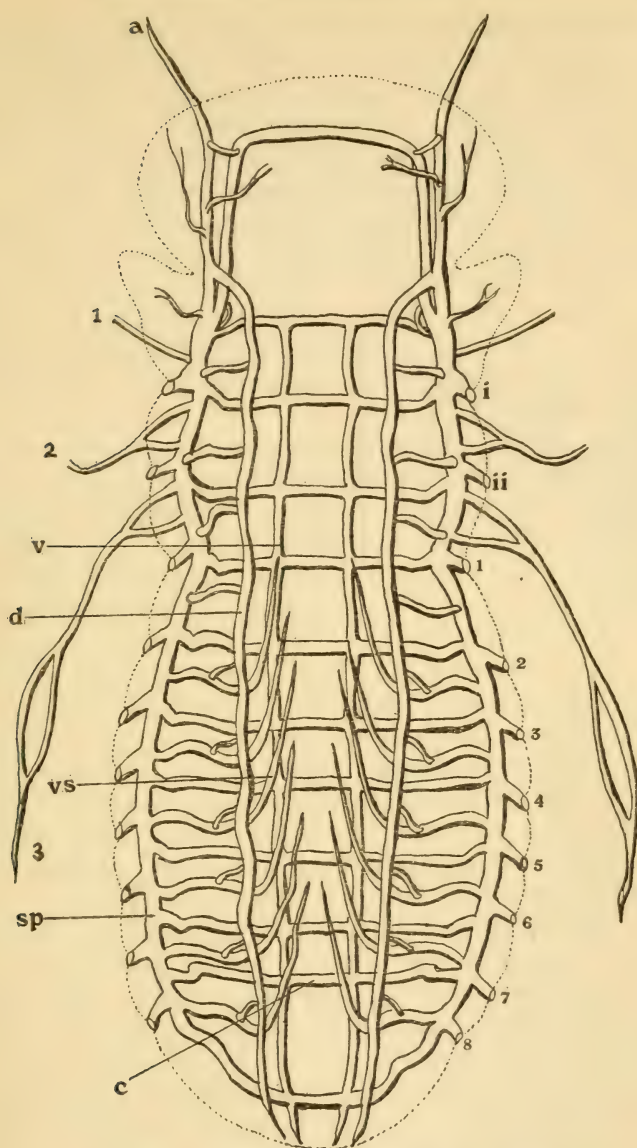


FIG. 14.—Magnified Diagram of the Tracheal System in a young Termite. *d*, dorsal, *sp*, spiracular, and *v*, ventral longitudinal trunks; *c*, commissure; *vs*, visceral branches; *a*, antennal branch. 1, 2, 3 (on left side), air-tubes of legs. *i*, *ii*, thoracic spiracles; 1-8 (on right side) abdominal spiracles. Adapted from C. Fuller, *Ann. Natal Mus.* iv, 1919.

of surrounding tissues so that the calibre of the tube must be reduced when the insect's body contracts, while there is elasticity in the lining which ensures expansion of the tube again when the pressure is withdrawn. The fine air-tubes lead into the minute tracheoles, through whose exceedingly thin walls the gaseous exchanges between air and tissues are carried on. Each tracheole (Fig. 46, *tr*) arises as a cavity in a cell of the tracheal epithelium, ultimately uniting with the cavity of the tube, the cell growing out as an elongate hollow thread. The insect's breathing system is adapted for bringing air-currents alternately into and out of these tracheoles, and the mechanism of the process is of great interest.

The air-tube system may be regarded as growing inwards from the paired series of openings (spiracles or stigmata, Figs. 14, 15) that are found on the sides of most of the body-segments in the great majority of insects; these spiracles indicate indeed where the air-tubes began to grow into the body from the outer skin (ectoderm) during the embryonic growth of the insect (see p. 154). Spiracles are commonly present on one or two of the thoracic and eight of the abdominal segments. In some primitive wingless insects—bristle-tails—the branching system of air-tubes arising from each spiracle remains distinct from all the others, but usually large longitudinal trunks run along the body connecting the successive spiracular tubes; more slender longitudinal trunks run dorsally along either side of the heart and ventrally along either side of the nerve-cord, while transverse commissures link up the right and left trunks so that the whole tracheal system forms a complex network. Each spiracle is surrounded by a rim of strong thick chitin, and the aperture is often guarded by a series of inwardly directed hair-like or spine-like processes which hinder the access of foreign bodies to the system. Just within the spiracle is a valve wherein by means of a specially thickened chitinous "bow," or a lever operated by suitable muscles the cavity of the spiracular tube can be closed (Fig. 15). The breathing of insects was well described by F. Plateau (1884)

and L. C. Miall (1886). The rhythmic contraction and relaxation of the spiracular muscles and the elasticity of their chitinous attachments cause the spiracular valves to open and close alternately. The contraction of the abdominal muscles, the details of whose arrangement vary in different groups of insects, reduces the capacity of the abdomen so that the organs press on the air-tubes; when the abdominal muscles are relaxed, the maximum capacity is restored through the elasticity of the body-walls. Thus it comes to pass that with the expansion of the body a small volume of fresh air passes in through the open spiracles to supplement the residual air always present in the tubes. When the spiracular valves close and the body contracts so that pressure is exerted on the tubes, air is

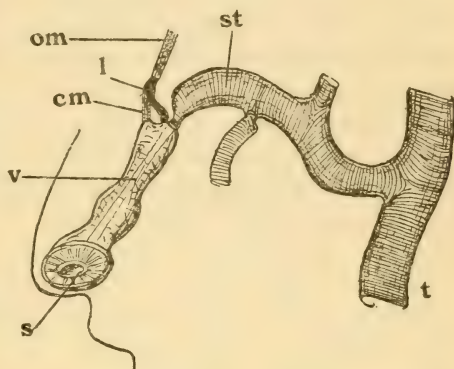


FIG. 15.—Abdominal spiracle and its connection with the tracheal system in a Louse (*Haematopinus*). *s*, spiracle; *v*, vestibule; *l*, lever; *cm*, closing muscle; *om*, opening muscle; *st*, spiracular trachea; *t*, part of longitudinal tracheal trunk.  $\times 200$ .

forced into the tracheoles. The opening of the spiracles while the body is still contracting ensures the expiration of a certain quantity of air, to be followed—when the abdominal muscles relax—by the inspiratory action already explained. The passage in and out of the inspired and expired air-current is accompanied by a twofold diffusion of gaseous constituents, oxygen passing from the fresh air wherein its tension is high to the tracheoles and tissues with their low oxygen tension, while the excess of carbon dioxide diffuses from the tracheoles to pass out of the spiracles with the expiratory air-currents into the atmosphere with its low tension of carbon dioxide.



The combustion processes that go on in the tissues of insects tend to maintain a fairly high body temperature. This becomes evident when a number of active insects are crowded together; the summer temperature of a beehive is over 90° F. and the winter temperature nearly 80°. Experiments on the gaseous exchanges of a number of bees whose thoracic air-tubes were choked with small parasitic mites (*Acarapis*, see J. Rennie, 1921) show that the output of carbon dioxide is in such cases very much below the normal, while the wing-muscles, largely deprived of their needed oxygen, are often incapable of normal action so that the insects cannot fly.

In insects of feeble or occasional flight, such as cockroaches, the whole tracheal system may be described as tubular; but in many insects of great activity and continual and powerful flight, capacious air-sacs of rotund or oval shape, are developed as enlargements of the main trunks or branches. Grasshoppers, flying beetles such as chafers, dragonflies, and bees are examples of insects with extensive air-sacs (Fig. 12, *ts*). The walls of these expansions are without the spiral thickening of the lining that characterises the tracheal system generally. It may be concluded that they serve as reservoirs of air from which the finer branches may be replenished.

Many and great modifications of the typical insectan breathing system are found to be correlated with special modes of life, particularly in the immature stages of those insects which pass through marked transformation in their life-history. These will be more appropriately considered in later chapters. But in this general account of the function of breathing an introductory reference is necessary to the means whereby insects living submerged in water obtain their supply of air. Many adult insects that frequently dive and swim under water—some aquatic beetles and bugs for example—carry down with them a supply of air, sealed beneath their firm forewings or as a bubble surrounding some part of the body giving access to the spiracles. Some aquatic larvae—like the familiar gnat-grub—have their hind-



most spiracles alone open, and these are situated on some outgrowth which can be thrust through the surface film of the water so as to make temporary contact with the upper air. But in other aquatic insect-larvae there is provision for using the air dissolved in the water by means of gills. In the grubs of mayflies and the slender dragon-flies (" damsel-flies ") one or more pairs of abdominal limbs—tubular or flattened in form with delicate cuticle and containing a network of branching air-tubes—serve for the passage of oxygen from the dissolved air into the tracheal system of the insect. These organs are distinguished as tracheal gills. In the larvae of caddis-flies and many midges there are delicate hollow finger-like outgrowths on the abdomen ; the cavities of these are prolongations of the great blood-space of the body and they are therefore known as blood-gills. In this case the blood-currents pass in and out of these gills, so that the blood serves as a carrier of oxygen to and of carbon dioxide from the tissues, as is usual in animals generally. The well-known " blood-worm " larva of the midge *Chironomus* (Miall and Hammond, 1900) has diffused through its blood-plasma the same respiratory pigment (haemoglobin, a compound containing protein and iron) that is characteristic of vertebrates. These midge-grubs spend much of their time burrowing in mud, and the affinity of the haemoglobin for oxygen, which it holds in loose combination, enables it to retain a store of that " vital " gas which can be renewed when the slender grubs rise towards the surface of their native pond, where the water is fairly well aerated.

Some midges of the *Chironomus* family have, however, larvae without any air-tube system at all, and there are many aquatic grubs in which the special breathing organs become well-developed only late in the process of growth. Such are able to effect gaseous exchanges through the thin and delicate body-wall, as many worms do. Their small size and excessively thin cuticle render any respiratory system needless. The same condition is found throughout life, in most members of the order of wingless insects known as

springtails (Collembola). These live mostly in sheltered situations, under bark, in soil, beneath stones, where they can effect directly through the skin and cuticle gaseous exchange with the surrounding moist air. The whole body in such cases appears to act as a blood-gill. But we have still much to learn as to the method by which these exchanges are brought about.

Enough has perhaps been stated to suggest how the living insect builds its tissues and obtains its sources of energy out of the materials supplied in its food, how it draws directly or indirectly on the atmosphere for its needed oxygen, and how it gives back to its surroundings the comparatively simple waste substances such as carbon dioxide, water, urates—the end-products of those internal changes that are a necessary accompaniment of its life.

## CHAPTER III

### MOVEMENT

ONE of the facts most easily to be noticed by the observer of living insects is that the vast majority of these creatures are constantly moving. According to its kind, its inborn habits, or its impressions received from the outside world, an insect walks or runs, creeps or swims, jumps or flies. These actions if carefully watched are seen to result from the beautifully co-ordinated movements of various parts of the exoskeleton. For example, when a beetle walks three of its six legs—the front and hind legs of one side with the intermediate leg of the other—are lifted and carried forward ; then the feet of these three limbs press the ground, and the other three legs are lifted and moved forward in their turn. If the movements of a single leg are watched it will be seen that the long stout segment or thigh is moved in relation to the body and that the adjoining more slender segment or shin moves in relation to the thigh, the angle between thigh and shin being alternately acute (when the knee joint is bent or flexed) and obtuse (when the knee joint is straightened or extended).

Such visible movements on the part of an insect are due to the longitudinal contraction of the specialised tissue that forms the muscles which, situated inside the legs or other parts of the exoskeleton, are so attached to these that by their power of longitudinal contractility they can move the parts in relation to each other. The fibrous structure of insect-muscles is readily seen on examination with a hand-lens, and a small fragment of such muscle, suitably treated, shows that it is composed of an enormous number of

fibres—slender contractile threads extending in the direction of the length of the muscle, which may thus be considered as composed of many bundles of fibres. It has already been mentioned (p. 2), that the muscles of insects resemble the skeletal muscles of vertebrates in being composed of striped or striated fibres (Fig. 16). With a comparatively low degree of magnification it is seen that these fibres exhibit alternating darker and lighter transverse bands; they are striated. On studying the structure of a single fibre with a high degree of magnification, it is seen in places to split lengthwise into

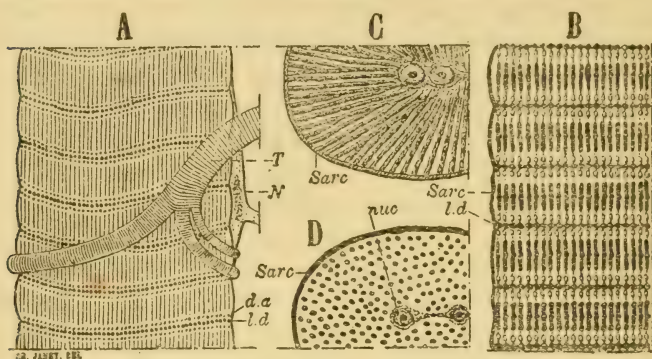


FIG. 16.—Microscopic structure of mandibular Muscle of Hornet (*Vespa crabro*). A, part of fibre treated with potash;  $\times 425$ . B, the same stained with haematoxylin. *Sarc*, sarcolemma; *ld*., Dobie's line; *da*, thickenings of fibrillae; *T*, air-tube; *N*, nerve end-plate. C, partial cross-section at Dobie's line showing radiating fibrils; D, partial cross-section through median region of a sarcomere showing fibrillae and nuclei (*nuc*).  $\times 850$ . From C. Janet, *Etudes sur les Fourmis les Guêpes et les Abeilles*, xii, 1895.

excessively fine threads or fibrils, while the cross-striation becomes so definite as to suggest that the fibre is built up of an innumerable series of discs arranged one on the other; a very rough model of its apparent structure might be made with a pile of pennies and half-crowns arranged alternately, and such transverse dissociation of a fibre can be brought about by treatment with gold chloride. But the fibre never splits naturally into discs as it does into fibrils, and the alternating darker and lighter transverse regions are indications of physical differentiation in the substance of the fibre.



The muscle substance is essentially protoplasm endowed with the special power of contracting. Each fibre is bounded by a delicate structureless sheath, the sarcolemma (Fig. 16), inside which nuclei can be distinguished; the fibre has therefore been formed by the coalescence of a large number of cells whose boundaries can no longer be detected. The striation of the fibres is comparatively coarse in the muscles of many insects and the structure has been minutely studied by various observers. According to the researches of C. Janet (1895) and E. Schäfer (1891) on the wing-muscles of ants, wasps, and beetles, each light stripe is traversed by a fine line (Dobie's line or Krause's "membrane" (Fig. 16, *ld*)) which sometimes appears broken (a "dotted line"). The portion of a fibril between two such lines is a sarcomere, and the central dark region of the sarcomere appears as a band or disc; the dark substance or sarcous element has a striped aspect because it is traversed by two sets of longitudinal pores which are open towards Dobie's line in either direction but closed towards the median plane of the sarcomere. The substance of the sarcous element, as well as the pores, becomes shorter and broader when the fibril contracts, longer and narrower when it relaxes; in the latter condition a clear transverse line (Hensen's line) may be distinguished in the median plane of the sarcomere. The paler and presumably more fluid constituent (hyaloplasm) of the sarcomere is largely absorbed in the pores during contraction and squeezed out of them during relaxation. An interstitial network with radially arranged filaments (Fig. 16, *c*) has been described in the neighbourhood of Dobie's line. The arrangement of the various constituents is such that contraction can take effect only in the longitudinal direction of the fibre. All the fibrils contract together and the amount of contraction of each fibril may be regarded as the sum of the contractions of the sarcomeres that compose it. Not that all the sarcomeres in a fibril contract simultaneously; a wave of contraction whose velocity can be measured passes along each fibre, and therefore along the whole muscle from end to end. The muscles of insects are, as we have already

seen, surrounded by blood which brings nutrient substances to the active tissue and removes waste products from it, and supplied with numerous fine branches (tracheoles) of the air-tube system through whose delicate walls oxygen passes into the muscle for support of the combustion processes that liberate the energy needed for contraction, while the carbon dioxide resulting from the combustion is diffused out. In outer contact with the sarcolemma are numerous discoid nerve-endings (Fig. 16, A, N) associated with nerve fibres along which travel the impulses which excite the muscle-fibres to contract, as will be elucidated in the next chapter.

The muscles of insects are not surrounded by tough connective-tissue sheaths like those of vertebrates; the bundles of fibres can be readily separated by teasing out, wherever a muscle is exposed by removal of some part of the exoskeleton. In many cases these fibres are directly connected with the portion of the exoskeleton which is moved by their contraction, but generally the muscle works on the skeletal sclerite through a tendon or a number of tendinous cords. These are cuticular structures secreted by inpushed portions of the skin which grow towards and find contact with the muscles. The insertion of a muscle by means of a tendon results in the pull due to its contraction being exerted on a certain special small area of sclerite; thus precision of action is ensured. In studying the mechanism of movement among insects, the arrangement of the firm regions of the cuticle which make up the exoskeleton is as important as the form and nature of the muscles themselves; the admirable accuracy of an insect's observable actions depends on the correlation of these two sets of organs. As an introductory illustration of such action the exoskeleton and muscles of the legs, already briefly mentioned, may be profitably studied.

The three pairs of legs of an insect are articulated respectively to the three thoracic segments. Each leg is seen to consist of a series of hard sclerites segmentally arranged with flexible tracts of cuticle at the joints between adjacent

sclerites, which are thus capable of movement in relation to each other (Fig. 17). The segment of an insect's leg next the body is the conical or subconical haunch (coxa), the broad base of which adjoins the sternal region of its segment while it tapers distally to its junction with the small sickle-shaped trochanter which is succeeded by the long stout thigh or femur. In some insects, cockroaches for example, the cuticle of the haunch is partly transparent so that the strong muscles which, by their contraction, move the leg as a whole can be seen through it, their white colour contrasting markedly with the general brown hue of the exoskeleton. The leg-muscles in the cockroach are described by Miall and Denny (1886). From the dorsal region of the thorax on either side muscles pass to the inner and outer edges of each haunch; these are respectively the *adductor* and *abductor coxae*, as by contraction of the former the leg is drawn in towards the axis of the body, while by contraction of the latter it is moved outwards. A very strong muscle with its basal attachment (origin) also on the thoracic skeleton traverses the haunch, its fibres converging to their distal attachment (insertion) by means of a tendon on the inner (convex) edge of the trochanter. This is the muscle whose contraction straightens the thigh in relation to the

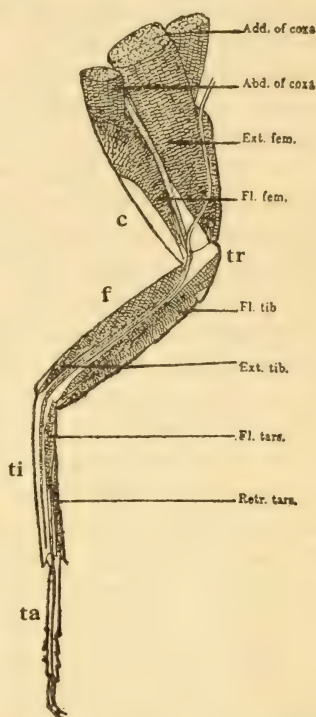


FIG. 17.—Left intermediate Leg of Cockroach (*Blatta orientalis*), showing segments and muscles. *c*, coxa; *tr*, trochanter; *f*, femur or thigh; *ti*, tibia or shin; *ta*, tarsus or foot. Muscles: *Add*, adductor; *Abd*, abductor; *Ext*, extensor; *Fl*, flexor; *Retr*, retractor.  $\times 3$ . After L. C. Miall and A Denny, *The Cockroach*, 1886.



haunch, trochanter and thigh moving as one piece ; the muscle is therefore known as the *extensor femoris*. It is readily understood that by the straightening of the leg with the foot resting on the ground the body of the insect is thrust forwards ; hence these muscles are of great importance in such actions as walking or running. A smaller muscle (*flexor femoris*) has its origin along the outer aspect of the haunch and is inserted by means of a tendon on the outer (concave) edge of the trochanter ; when this muscle contracts the thigh is bent towards the haunch, a movement which lifts the foot from the ground and draws it forward in preparation for the subsequent repetition of the extending and propelling action. Within the thigh are two muscles whose fibres converge from their origin along the outer and inner edges of that segment to tendinous insertions on the corresponding edges of the base of the next leg-segment, the shin (tibia) articulated to the thigh at the flexible knee-joint ; these muscles are respectively the *extensor* and *flexor tibiae*, their function respectively being to straighten or bend the leg at the knee. Beyond the shin follows the foot (tarsus) with its five segments, the first the longest and the fifth longer than any of the three intervening. A muscle (*flexor tarsi*) originating along part of the inner edge of the shin has its fibres converging into a long tendon which traverses the successive segments of the foot and is inserted into its tip ; when this muscle contracts the foot is curled or bent by the flexion of all its segments in the same direction. There are also two other muscles in the shin, the *protractor* and *retractor tarsi* ; these are inserted at the base of the foot respectively in front and behind, and their action is to swing the foot backwards or forwards in relation to the rest of the leg. The backward swing of the foot clearly assists in the forward propulsion of the body in walking or running. Each foot-segment has a patch of white cuticle below its terminal region ; this gives some power of adherence to smooth surfaces, and the patch (*pulvillus*) at the tip of the foot is larger and more conspicuous than the others. The terminal foot-segment carries a pair of strong



curved claws, which can be flexed by the tendon of the *flexor tarsi* muscle, and are of use in affording the insect a hold on rough surfaces. In the act of walking all these various muscles in the creature's six legs are brought into play, the contractions synchronising or alternating rhythmically so as to bring about the orderly movement of the legs in two sets of three as already mentioned

Besides walking and running, many insects have other modes of movement by means of their legs, such as leaping, gliding, or swimming. In a grasshopper the hindmost legs are by far the longest and strongest of the three pairs. When such an insect is at rest these limbs are seen to be strongly flexed at the knee joint; the sudden extension of the shin, brought about by contraction of the large muscles within the swollen thighs, propels the insect for a distance of several feet through the air. Fleas are notorious for their power of leaping; in their legs the haunches are exceptionally long as well as stout, and the flea's jump is due to the extension of the thighs. Aquatic insects such as water-beetles which swim and dive have either the intermediate or hind legs or both pairs flattened so as to serve as oars or paddles. The thighs move on the haunches and there is little change in the relative position of thigh and shin, as the strong limbs are swept rhythmically forwards and backwards. It is noteworthy that in these jumping and swimming actions the two legs of a pair move together, not alternately as in a walk or run.

By means of suitably arranged muscles many parts of the trunk can be moved in relation to one another. The dorsal sclerites (terga) of the abdomen are linked up by longitudinal strands of muscle the *abdominal tergals*, as the ventral sclerites (sterna) of the same region by sheets of *abdominal sternals*, while vertically directed *tergo-sternal* muscles connect each tergum with the sternum of its segment. By the contraction of the last-named muscles the dorsal and ventral walls are drawn together, the capacity of the abdomen being thus reduced and the pressure necessary for respiration exerted on the air-tubes (see pp. 42-3 above).

When both sets of the longitudinal muscles of the abdomen contract, that region is shortened by a partial telescoping of the segments ; contraction of the abdominal tergals tends to straighten the abdomen or to bend the tail upwards, while contraction of the sternals flexes the abdomen ventralwards. There are also short *oblique tergal* and *sternal* muscles inserted laterally, which when they contract bend the abdomen to one side or the other.

In many insects during the early (larval) stages of their life-history, when the limbs are relatively small or even wanting, these muscles connecting adjacent segments are the main agents in locomotion. By stretching out the head region and then drawing the rest of the body after it by waves of contraction, the characteristic creeping movement of a grub or maggot (Plate II, D) is brought about.

A moderately full account of the muscular system of any insect would be far beyond the scope of this book ; one of the famous past-time students of insect anatomy, Pierre Lyonet (1762), dissected out and described sixteen hundred and forty-six muscles in the caterpillar of the Goat Moth. These muscles, like the other organs of immature insects which have to pass through a transformation before attaining maturity, are arranged so as to be specially adapted for the insect's activities during the larval period of its life, and these are commonly widely different from the activities of the creature when adult.

Most insects when fully grown have the power of flight, and the action of the wings is therefore among the most characteristic and remarkable of all the movements of insects. The wing of an insect of powerful flight, such as a dragon-fly, appears to be a sheet of firm, transparent membrane stiffened by tubular "veins" or nervures. Study of the method of wing-growth, however, shows that a wing arises as a pouch or outgrowth from the dorso-lateral region of the thoracic segment that bears it. This pouch becomes flattened and in the developed wing the two folds—"roof" and "floor" as they might be called—come into close apposition over the greater part of the surface, which is

covered by firm cuticle. Air-tubes, however, grow into the pouch or wing-rudiment during its development, and these become surrounded by the thickened tubular structures which appear as the supporting nervures of the wing (Fig. 18). As development proceeds the cells of the skin (Fig. 18, B, *e*), which are active in forming the cuticle, become attenuated and at length disappear, so that the adult wing is entirely cuticular.

A fully developed wing is jointed to the thoracic segment from which it arises, the forewings belonging to

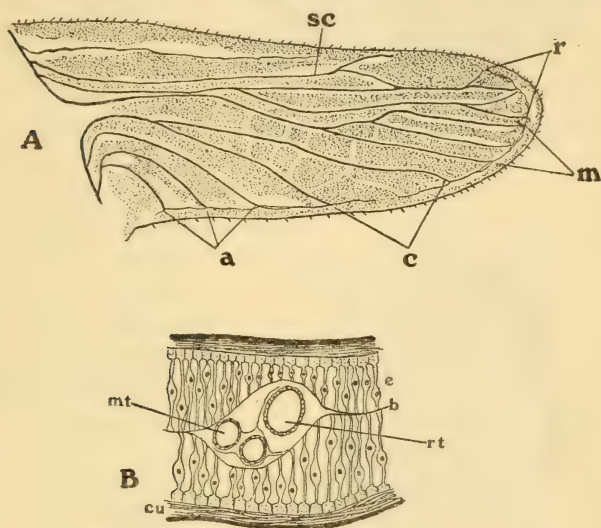


FIG. 18.—A, Forewing of nymphal Stone-fly (*Taeniopteryx*) showing the tracheal trunks and their branches (*sc*, subcostal; *r*, radial; *m*, median; *c*, cubital; *a*, anal). The pale tracks indicate positions of developing nervures.  $\times 12$ . B, cross-section through developing wing of a Dragon-fly nymph (*Anax*). *cu*, cuticle; *e*, epidermis; *rt*, radial trachea; *mt*, median trachea.  $\times 150$ . After J. H. Comstock and J. G. Needham. *Amer. Nat.* xxxii, xxxiii.

the second (mesothorax) and the hindwings to the third segment (metathorax) of that region of the body. The base of the wing, its region of attachment, is relatively small and is supported by a series of sclerites which are connected by flexible cuticle to the thoracic wall, so that the wing is



free to move up or down, to spread so as to project outwards from the axis of the body, or to be drawn inwards so that

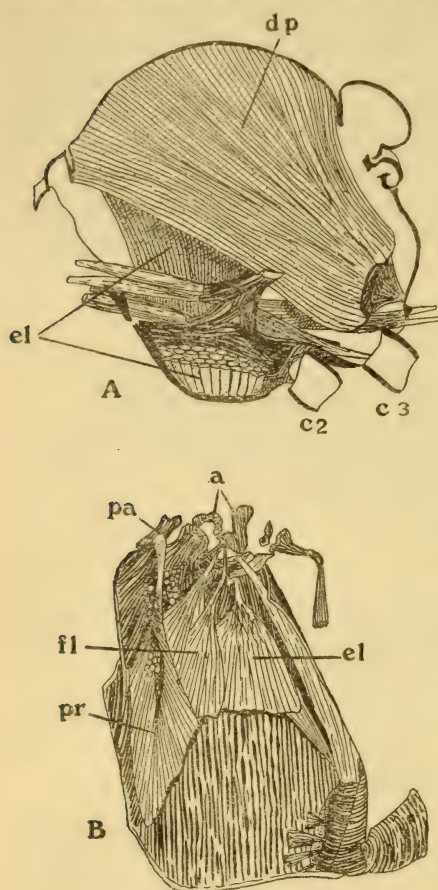


FIG. 19.—Principal Wing Muscles of male Honey Bee (*Apis mellifica*), as seen in median section through thorax (A), and internal view of right pleuron of mesothorax (B). *el*, elevators; *dp*, depressors; *pr*, pronator; *fl*, flexor muscles; *pa*, parapterum; *a*, axillary sclerites. *c<sub>2</sub>*, *c<sub>3</sub>*, haunches of second and third legs.  $\times 15$ . After R. E. Snodgrass.

to the wing-base but to regions of the thoracic wall. The

its length is approximately parallel to that axis as well as to be partly turned on its axis so that its lower aspect is directed backwards. The spreading and indrawing movements are brought about respectively by extensor and flexor muscles inserted at the wing base. The forward turn of the wing-surface is due to the action of *pronator* muscles (Fig. 19, B, *pr*) inserted into a sclerite (*anterior parapterum*) at the front costal wing-base, and also to the resistant action of the air on the flexible wing-membrane. But the large and powerful muscles which by their contraction move the wings up and down are in the vast majority of insects attached not directly



*elevators* of the wing are muscles with fibres running almost vertically (Fig. 19, *el*) between the ventral and dorsal aspects of the thorax ; when they contract they pull the dorsal wall down, the wing-base is necessarily pulled down and the wing-tip rises. The *depressors* of the wing (Fig. 19, A, *dp*) run obliquely along the thorax so as to pull part of its wall backwards ; this raises the dorsal region with the wing-bases, and so the wing generally is depressed. In dragon-flies the great wing muscles are attached to the sclerites of the wing-bases so that they act directly on the wings as on levers. Their arrangement, three elevator and five depressor muscles to each of the four wings, has been described in detail by R. von Lendenfeld (1881). H. R. A. Mallock (1919), commenting on this remarkable contrast in the working of an essential group of muscles in dragon-flies as compared with other insects, writes : " The question arises as to why has this complicated and indirect method prevailed ? If the problem were set of designing a mechanism for flapping wings, the dragon-flies' solution would certainly be the first to suggest itself ; yet it evidently must have some disadvantages since it has not been generally adopted." It may be suggested that the flight muscles, attached between various regions of the thoracic wall, though acting indirectly on the wings are perfectly correlated with the articulation of these to the thorax, and that such mode of attachment is less delicate and liable to derangement than the direct action which characterises the dragon-flies. In Locusts, Grasshoppers and their allies there are direct elevators and depressors inserted at the wing-bases, as well as the indirect muscles attached to the thoracic wall. It is noteworthy that dragon-flies, while remarkably powerful, swift and accurate fliers, have no provision for coupling the two wings of one side together when flying ; the forewings and hindwings are worked by independent sets of muscles and the co-ordination of the wings of the two pairs depends upon an internally placed lever connecting their basal sclerites, and correlation in nervous control. In the more primitive insects of other orders also, such as Orthoptera (Cockroaches

and Grasshoppers), Plecoptera (Stone-flies), Isoptera (Termites), the wings of the two pairs are uncoupled and each wing-bearing segment has its own set of thoracic muscles. But, on the other hand, in the great majority of highly organised flying insects of other orders there is some form of wing-coupling apparatus, so that the fore and hind wing of each side move in unison, following the rhythmic changes of outline of the thorax due to the alternate contraction of the sets of flight-muscles. Thus among the bees,

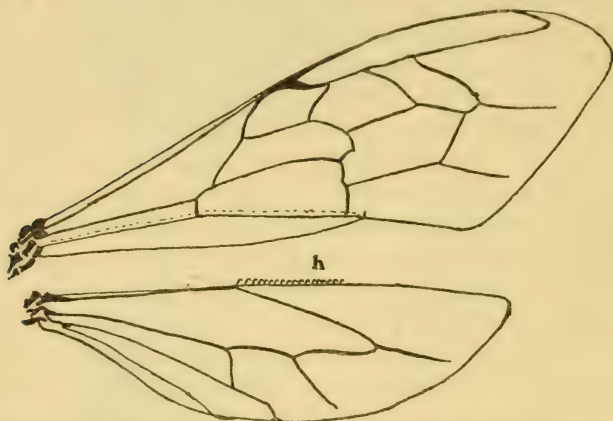


FIG. 20.—Right wings of Honey Bee (*Apis*). *h*, row of hooklets on costa of hindwing which hold dorsal edge of forewing during flight.  $\times 8$ . After Comstock and Needham and Snodgrass.

wasps, and other insects of the order Hymenoptera a series of curved hook-like bristles along the front edge (costa) of the hindwing catch on the thickened hind-edge (dorsum) of the forewing (Fig. 20); it is easy to demonstrate this linkage by manipulating the wings of a large wasp or sawfly. In some of the Lacewing and Scorpion-fly groups (Neuroptera and Mecoptera), as R. J. Tillyard (1920) has pointed out, there is a lobe or process (jugum) at the hind-base of the forewing, and on the costa of the hindwing a corresponding humeral lobe bearing one or two stiff bristles (frenulum). The jugum is present also in many Trichoptera (Caddis-flies) and in a few Lepidoptera (Moths), though in

the vast majority of families of this great order we find a well-developed frenulum composed of numerous bristles closely apposed, projecting from the costal base of the hind-

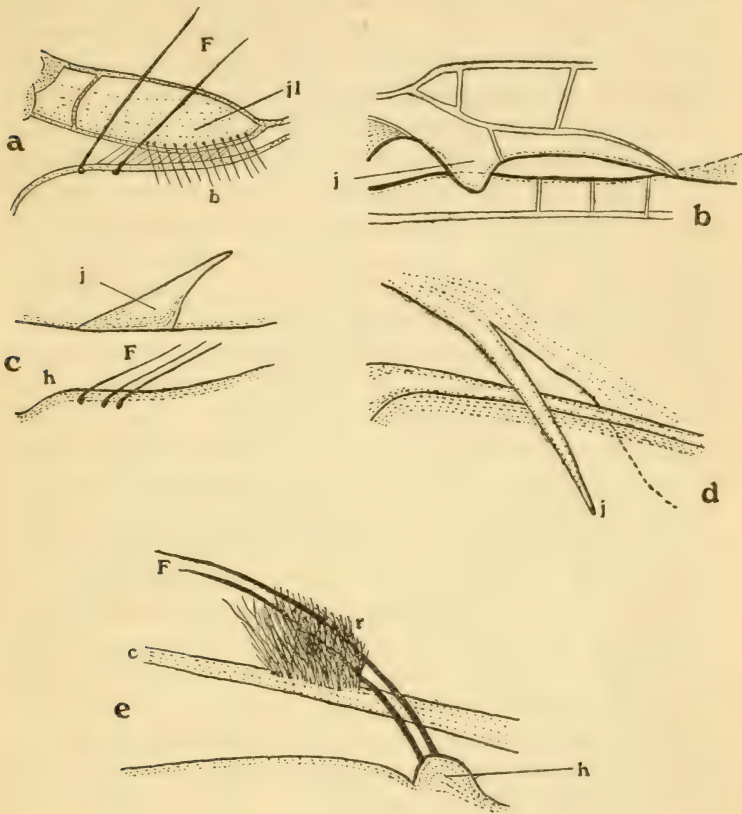


FIG. 21.—Types of Wing-coupling Apparatus in various Insects. *a*, Mecoptera (*Taeniochorista*),  $\times 80$ ; *b*, Neuroptera (*Archichauliodes*),  $\times 10$ ; *c*, Lepidoptera (Micropterygidae: *Sabatinca*),  $\times 80$ ; *d*, Lepidoptera (Hepialidae: *Charagia*),  $\times 14$ ; *e*, Lepidoptera (Noctuidae: *Plusia*),  $\times 30$ . *jl*, jugal lobe; *j*, jugum; *b*, jugal bristles (on forewing); *h*, humeral lobe, and *F*, frenulum (on hindwing); *r*, retinacular bristles on cubital nervure (*c*) of forewing. After R. J. Tillyard. (*Proc. Linn. Soc. N.S.W.* xliii, 1918.)

wing and fitting beneath a number of stiff hairs or scales under the base of the forewing (Fig. 21, *e*). Through such



arrangements the two wings of a side are coupled and present an extensive surface to the air, which is compressed as they are pulled downwards by means of the depressor muscles, and turned backwards by the action of the flexors and by the wing's elasticity. This atmospheric compression leads to the resistance which is the mechanical agent in supporting and propelling the insect during flight. Then in the great order of the two-winged flies (Diptera), the forewings alone are developed as organs of flight, while in the beetles and earwigs the hindwings only are efficient, the forewings being modified into firm sheaths (elytra).

Our knowledge of the mechanism of insect flight is largely due to the researches of E. J. Marey (1895), who by obtaining tracings of the wing-tips of flying insects on the smoked cylinder and fastening a spangle of gold leaf to the tip of the wings, vibrating as in flight, of a wasp held by forceps in bright sunlight, demonstrated that the path (trajectory) of the wing-tip is a narrow and elongate "figure of eight." Marey's work has been supplemented by the special studies of F. Stellwaag (1910) and W. Ritter (1911) on the flight of the hive-bee and the blow-fly respectively. In the latter insect there are ten directly-acting muscles attached to the sclerites of each wing-base ; these though not working as the depressors and elevators of the wing, are of much importance in effecting the suitable tension of the wing, and possibly act in steering.

Observation of insects during flight affords to the student abundant opportunity of noticing how the details of wing movement vary in different groups. How markedly, for example, does the heavy flapping flight of many of our larger butterflies contrast with the darting movement, alternating with the apparently motionless poising in the air, of a "Humming-bird" Hawk-moth or a hoverfly ! In the former case the number of wing-strokes per second might be roughly calculated by observation ; in the latter they can be determined only by tracings on smoked paper compared with those made by a tuning fork of standard vibration rate, or, if the wing-vibrations produce an audible hum, by verifying



the musical note in unison therewith. Thus it has been found that a Common White Butterfly (*Pieris*) makes only nine wing-strokes a second as contrasted with the 190 strokes a second of the Hive-bee (*Apis*), or the 330 strokes a second of a Housefly (*Musca*).

Relatively large insects with extensive wing-area and powers of prolonged, often soaring flight, have a rate of wing-motion intermediate between these extremes. A dragonfly, for example, may beat its wings twenty-eight times a second as it hawks through the air in pursuit of its prey. The different instances mentioned may serve to illustrate how, in every case, the special features of an insect's flight correspond with its peculiar way of life. Further consideration of flight in relation to the general behaviour and environment of insects may be deferred till a later chapter.

Walking, running, leaping, crawling, and flying are obvious modes of movement which cannot be overlooked by the most casual observer of insects. But there are many other movements of equal importance to the creature's life, which, though less conspicuous, are all brought about by muscular action. An insect continually moves its feelers as though seeking to test the neighbourhood into which it advances; these movements are due to the contraction of small muscles passing from the inside of the head-capsule to the feeler's basal segments. The feelers are, as already stated, modified limbs in series with the insect's legs. The three pairs of jaws (mandibles, maxillae, and labium) whose position and action were briefly described in the last chapter (pp. 17-23) in relation to the function of feeding, are likewise modified limbs. The muscles by which these jaws are worked are often numerous and always, in view of their use in nutrition, important. Some description of their arrangement may therefore be given first in a biting and then in a sucking insect.

The jaws and their muscles in the cockroach, a typical biting insect, have been described in detail by J. Mangan (1908). The Cockroach's mandible with its apical teeth and molar area, its convex and concave articulations (condyle

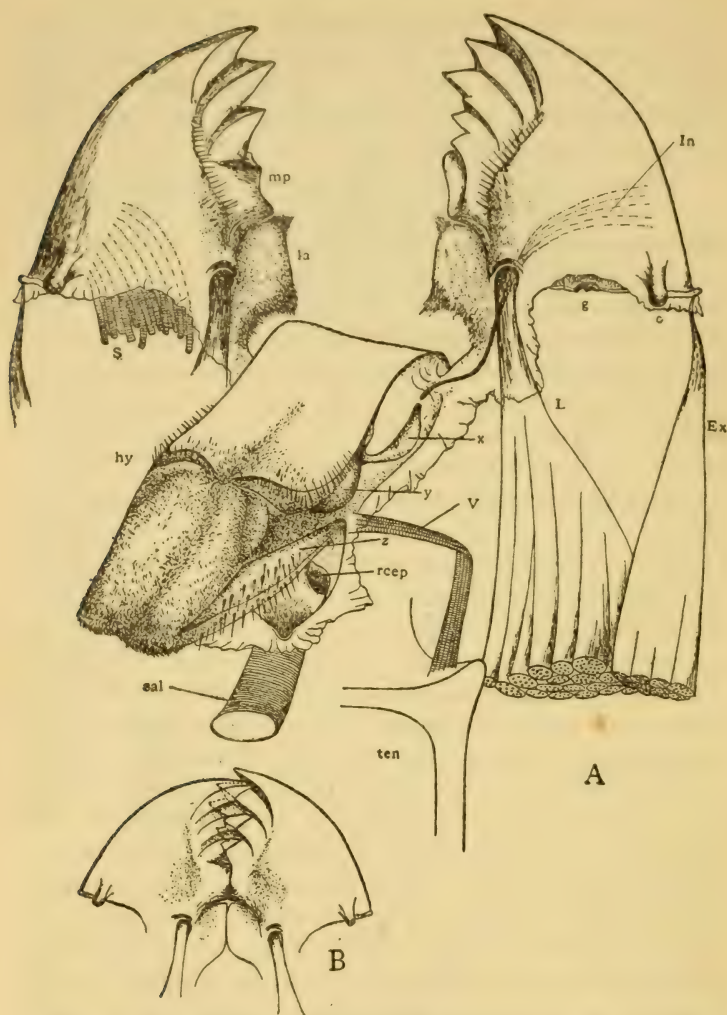


FIG. 22.—A, Mandibles and tongue (hypopharynx) of Australian Cockroach (*Periplaneta australasiae*), viewed from behind. *c*, condyle ; *g*, ginglymus ; *mp*, molar area ; *la*, lacinia of mandible. *L*, adductor muscle ; *Ex*, abductor ; *S*, short adductor. *hy*, hypopharynx partly turned backwards ; *x*, *y*, *z*, its sclerites (*z* probably the superlingua or paragnath) ; *In*, protractor and *V*, retractor muscle of tongue. *ten*, tentorium (internal head skeleton) ; *rcep*, salivary receptacle.  $\times 24$ . B, The mandibles closed with teeth interlocking.  $\times 15$ . After J. Mangan (*Proc. R. I. Acad.* xxvii, 1908).

and ginglymus) with the head-skeleton, resembles that of the Earwig previously described (pp. 17-19). The mandible (Fig. 22) is pulled outwards by its abductor muscle (*Ex*), which consists of several bundles of fibres arising from the upper lateral region of the head capsule, and converging to a chitinous tendon inserted at the outer edge of the mandible beyond the condyle. The large adductor (*L*) which pulls the mandible inwards to meet its fellow of the opposite side is a much thicker and stronger muscle than the abductor; its numerous bundles of fibres arise from the top and back of the head-capsule, and converge to a strong chitinous tendon which is inserted in the hind inner region of the jaw. Each mandible has also a short adductor (*S*) whose parallel fibres pass directly from the inner head skeleton (tentorium) to the inner face of the mandible's convex outer wall. The contraction of these two adductors pulls the mandible in towards its fellow, so that the pair of jaws meet, with their teeth interlocking, opposite the centre of the mouth (Fig. 22, B), unless some food substance happens to lie between them; in such case the teeth cut it, and the molar areas grind it into small fragments.

The outer edge of the mandible has another muscle (*In*) of small extent whose fibres are fastened to its inner aspect. These converge into a long slender tendon which is inserted into the side of the tongue. This pair of muscles (*levatores linguae*) serve by their contraction to protrude the tongue. They are opposed by another pair of muscles (*retractores linguae*) which, passing from the tentorium on either side to the base of the tongue, pull that organ backwards into the mouth (Fig. 22, V).

The complex structure of the maxillae (see previous chapter, p. 19, and Fig. 23) necessitates a corresponding elaboration in the muscular system by which their parts are worked. Inserted into each cardo is a strap-like depressor muscle (*W*) with three sections arising from the tentorium. This depressor, by its contraction pulls the cardo and thus the whole maxilla downwards. An elevator or abductor (*P*) runs from the top of the head-capsule (epicranium) to the



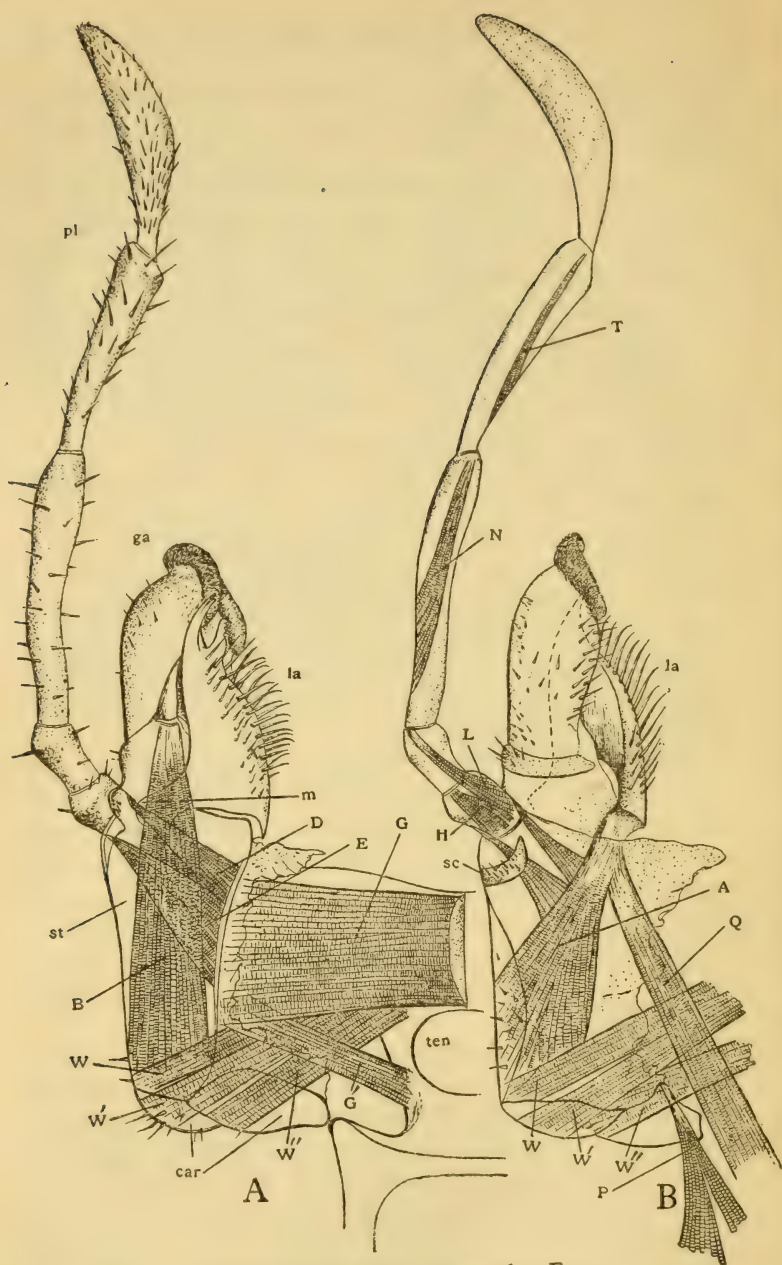


FIG. 23.—Maxillae of Australian Cockroach. For explanation, see opposite page.



cardo, and raises the maxilla. From the tentorium a broad strap-like muscle (*G*) passes to the stipes which it pulls, when contracting, towards the centre of the mouth ; this is the adductor of the stipes (and necessarily of the lobes carried by it) which it moves on the hinged articulation with the cardo. From within the stipes arise two long, thick tapering muscles (*A*, *B*), one the adductor of the lacinia and the other of the galea to the bases whereof they are respectively attached, the action of the latter being aided by another muscle arising from the tentorium. Two smaller muscles (*D*, *E*) passing from the inner edge of the stipes to the upper and lower edge of the palpiger are respectively the adductor and abductor of the palp as a whole, while the individual segments of that leg-like region are worked by slender muscles concealed within it. Thus the movements of the palp in testing objects over which the insect walks, as well as the action of the maxillary laciniae or blades in breaking up foodstuffs into finely divided particles are brought about.

The arrangement and mode of working of the head muscles are necessarily strongly modified in the case of jaws adapted for piercing and sucking. As an example we may take the jaws of a plant-bug such as *Lygus pabulinus* described in detail by P. R. Awati (1914). The mandibles and maxillae of insects of this order are elongate piercing stylets working to and fro in the dorsal groove of a jointed beak which is the modified labium. For the pulling back of these piercing jaws, there are retractor muscles which arise from chitinous rods in the dorsal region of the head-capsule, and are inserted into the swollen bases of the mandibles and maxillae respectively (Fig. 24A, *r*, *rx*). The jaws are thrust out, so

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FIG. 23.—Maxillae of Australian Cockroach (*Periplaneta australasiae*). A, right maxilla from behind ; B, left maxilla from front. *car*, cardo ; *st*, stipes ; *la*, lacinia ; *ga*, galea ; *p*, palp ; *m*, articulation of lacinia. *ten*, tentorium. Muscles : *A* and *Q*, adductors of lacinia ; *B*, adductor of galea ; *D*, adductor, and *E* abductor of palp ; *H*, *L*, *N*, *T*, segmental muscles of palp ; *G*, adductor of stipes ; *P*, elevator, and *W*, depressor of cardo. × 24. After J. Mangan (*Proc. R. I. Acad.* xxvii, 1908).

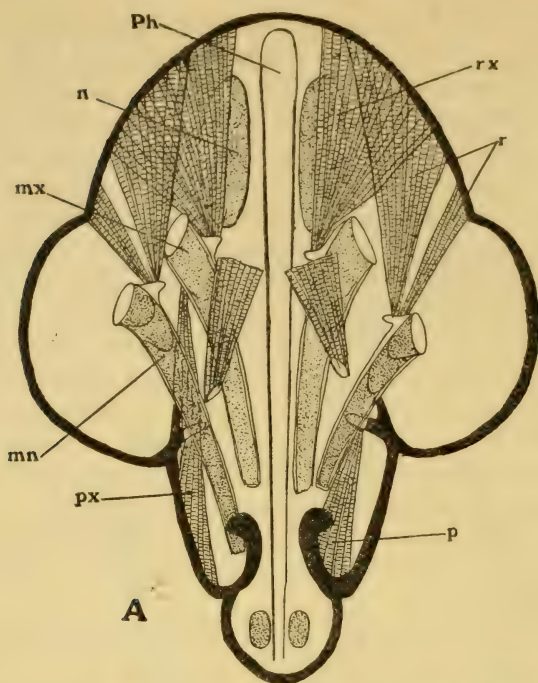


FIG. 24A.—Cross-Section through Head of Plant-bug (*Lygus pabulinus*); *Ph*, pharynx; *d*, its divaricator muscle; *g*, gullet; *ps*, salivary pump; *mp*, its muscle; *sd*, salivary duct; *r*, retractor, and *p*, protractor muscles of mandible (*mn*); *rx* and *px*, retractor and protractor of maxilla (*mx*); *l*, labial muscle; *b*, brain; *s*, sub-oesophageal ganglion; *n*, nerve-commissure; *o*, taste-organs.  $\times 200$ . After P. R. Awati, *P. Z. S.* 1914.

as to perforate the plant tissues and procure a supply of food-sap by the contraction of protractor muscles, which arise from the frontal ventral head-skeleton, and are inserted, in the case of the maxillary protractors (*px*), directly into the swollen bases of the jaws, but for the mandibular protractors (*p*) into transverse chitinous rods attached to the bases of the mandibles, and therefore pulling these as by the agency of levers. The labial beak, in which the mandibles and maxillae are thus pulled in or out, can be moved forwards and backwards by elongate muscles which pass from the dorsal wall of the prothorax to the front and hind aspect of the base of the terminal segment of

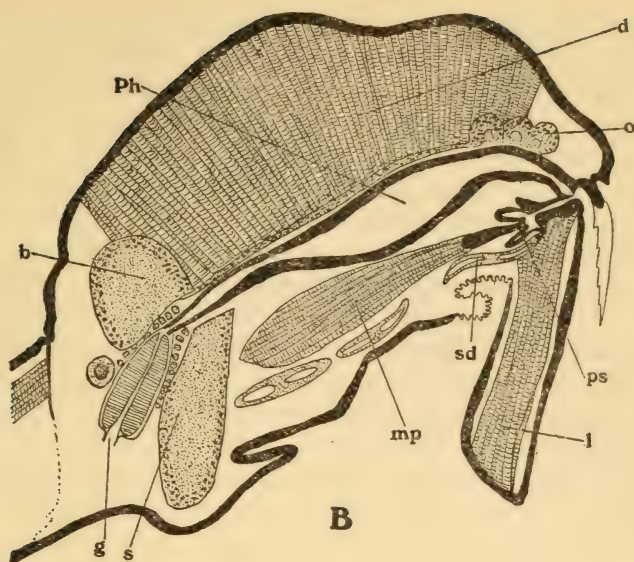


FIG. 24B,—Longitudinal Section through Head of Plant-bug For explanation, see Fig. 24A.

the beak. The liquid food obtained by the piercing action of the jaws is sucked in by movement of the walls of the pharynx, the region of the food-canal into which the mouth opens and from which the gullet leads out. There is a group of divaricator muscles (*d*) passing from the inside of the facial head region to the front wall of the pharynx; the contraction of these increases the capacity of the organ. They are antagonised by lateral pharyngeal muscles which arise from the head skeleton on either hand and are inserted into thickly chitinised paired regions of the pharyngeal wall. When these are pulled apart by the contraction of the lateral muscles, the dorsal and ventral walls of the pharynx are drawn closely together, and the cavity is almost obliterated.

For the digestion of an insect's food, movement of the walls of the digestive canal are necessary, and the action of the muscular layer of the proventriculus in constricting its aperture has been discussed in the previous chapter

(p. 27). Similarly contractions of the thin muscular wall of the heart are effective in propelling the blood, while by the action of the abdominal muscles changes in the form and capacity of the body are brought about so that through varying pressure on the tracheal tubes air is drawn in and expelled, the spiracles being rhythmically opened and closed by means of their special musculature. Only a glance at the highly complicated muscular system of an insect has been possible, but it will be realised that the actions of the various parts of this system must be co-ordinated if the creature's movements are to have purposeful relation to the needs of its life. Some discussion of the mode of such co-ordination will be found in the succeeding chapters.



## CHAPTER IV

### SENSATION AND REACTION

THE various movements of insects, some of which have been considered in the previous chapter, are often observed to be expressions of the creatures' responses to various kinds of stimulation due to the condition of their surroundings. A moth flies in through an open window on a summer night, steering a straight course for the lamp, so that the observer exclaims that the insect is "attracted by the light," and concludes that it possesses a faculty resembling at least to some degree his own power of vision. He may go several steps farther in equating the insect's behaviour and sensations with his own by saying that "it prefers light to darkness," or that "it is dazzled by the glare of the lamp." Collectors of insects desirous of obtaining male specimens of certain rare moths often take into the open country or woodlands a live female of the kind desired shut up in a box, and find that this miniature prison may be surrounded by large numbers of males which have directed their flight towards it. The captive female, though invisible, has allured them, and the observer may reasonably infer that these males have been thus "assembled" because they have received impressions accompanied by some recognised sensation analogous to our sense of smell. Reactions of insects to their surroundings, such as the two just mentioned, can be readily observed, and by study of the nervous system and its connection with the various parts of the body it is possible to understand, at least in part, the mechanism by which the various reactions are brought about. But when we ascribe to an insect sensations, or.

still more, intentions and apprehensions like our own, we quickly pass into regions of speculation, as we can no longer be guided by carefully tested fact. An insect may react to its surroundings in somewhat the same way as a man reacts, but it is not justifiable to infer from this that the insect's state of consciousness is like the man's. The questions thus raised are interesting, even fascinating, despite their difficulty. Before attempting to discuss them it will be well to consider in detail some examples of the working of stimulation and response in the insect's body.

A brief general sketch of the insectan nervous system has been already given in the first chapter (pp. 7-10) of this book, and it was there mentioned that movements such as the moth's flight towards a lamp or towards a female of his kind shut up in a box, movements clearly to be regarded as responses to stimulation from without, are called reflex actions. In a reflex action some nerve-ending, usually near the body surface and capable of being stimulated through a specialised region of the cuticle, is affected so that it transmits through a nerve-fibre an impulse to a nerve-centre such as part of the brain or a ventral ganglion. From the nerve-centre the impulse is then reflected along other nerve-fibres, whose endings in contact with muscle-fibres, impel these to contract and thus give rise to visible movement. Such movement is the result of, and to the observer affords evidence for, the transmission of the nerve-impulse to and from the nerve-centre. Impulses towards the centre, as well as the fibres along which they travel, are usually defined as afferent, while impulses from the centre to the muscles and also the nerve-fibres conveying them are called efferent.

An insect's nervous system may be regarded as a vast complex of living cells from each of which processes branch in various directions, many of these processes passing into the axes of nerve-fibres. In every nerve-centre a number of cells are grouped, and the fibres, whose axes are the prolongations of these cells, are bound into the white thread-like cords, evident on dissection, which are called nerves : every nerve is a bundle of many fibres. A nerve-

impulse passes from cell to cell along the path of the connecting fibres, a fibre-axis at its extremity coming into touch by means of exceedingly minute branches with relatively short finely branched outgrowths from other cells; thus a nerve impulse is passed on through a series of "cell-relays." An insect's apparently purposeful movements are therefore dependent on the co-ordinated transmission of a large number of impulses through the various parts of its nervous system, from receptive nerve-endings to the ganglia and thence to the muscles.

The nerve-endings of insects that can be affected by outward stimulation are of many kinds, adapted for the reception of varied types of influence. Attention has been repeatedly directed to the horny cuticle which covers an insect's body, and mention has been made of the hairs and spines—often long and conspicuous—which are specialised portions of the cuticle, jointed on to the main surface by basal flexible membrane (Fig. 1). Many hairs are hollow, and into their cavities pass fine thread-like processes of nerve-cells lying in the skin, whence nerve-fibres lead to groups of cells, situated in some ganglion. Such nerve-endings as these are clearly adapted for receiving tactile impressions. The slightest contact of any outside object with the hollow hair must lead to stimulation of the included thread-like process. Thus the skin-cell is affected, and from the cell the impulse passes along the nerve-fibre to a ganglion cell. Various objects that may be touched will necessarily cause many nerve-endings to be affected, and thus a number of impulses will simultaneously travel to a ganglion, where, through the linkage of the receptive cells, they will be co-ordinated and the impulses passed on to motor cells, whence by efferent fibres they will be reflected to the muscles whose contraction will result in the reaction appropriate to the stimulation received. The feelers carried on an insect's head, the palps connected with the jaws (maxillae and labium) as well as certain abdominal appendages such as the tail-feelers (cerci) are often richly provided with tactile organs, so that



the creature is exceedingly sensitive to impressions derived from objects touched. Sensory hairs and spines are also often present on the cuticle of various segments of the body, especially in the case of those insects whose exoskeleton is relatively weak, so that prompt response to impressions from all quarters is essential to secure safety. Many insects, as they walk or run, may be seen to keep the tips of their feelers in continual swaying movement, which has the effect of bringing the sensory hairs on the segments of the feelers in such relation with surrounding objects that there are abundant possibilities of varied points of contact. And the response of the whole insect to the impressions thus received depends upon the positions of the various sensory hairs where these impressions are started through contact with external objects.

The nerve-endings affected through such hairs are termed tactile, and their mode of action suggests that insects possess a "sense of touch." It is certain that these nerve-endings are affected when the hairs within which their extremities lie come into contact with outside objects, and the insect's reaction to such stimulation, due to muscular contraction, shows that a reflex impulse travels to and from the central nervous system. So far there is analogy between what happens in the insect and in a human being. But what we understand by a sensation which leads us to distinguish an object as hard or soft, rough or smooth, is essentially a conscious experience, accompanying certain nerve-impulses, but not identifiable with them. We are not, therefore, able to assert that an insect "feels" as we do. Indeed, the insect's tactile nerve-endings are in form very different from those of vertebrates and are affected in a different manner. A tactile corpuscle of the human finger, for example, is situated beneath the outer skin (epidermis) and is affected indirectly by variations of pressure or resistance acting at the surface of the skin yet able to "irritate" the nerve-ending, though the latter lies under many layers of cells. The insect's tactile nerve-ending is, as we have seen, prolonged so as to rest within a narrow hair; it is



therefore directly pressed or bent when the hair touches an external object. As far as physiological mechanism can guide us, we may conclude that the insect's reception of and reaction to tactile stimulation are far more delicate than our own. But we have no evidence that an insect's "sense of touch," experienced in whatever form of consciousness the creature may possess, is more vivid than ours, or indeed that it is like ours at all.

Besides these "sensory" hairs and spines whose function is undoubtedly tactile—that is to say, the nerve-ending can be stimulated only if the hair actually touches some external object—the feelers and parts of the jaws of many insects carry blunt peg-like outgrowths of the cuticle in which the chitin is markedly thinner than in typical tactile hairs. Into the cavity of those also pass delicate processes of nerve-cells in the skin. Most students of the sense-organs of insects—for example, A. Forel (1908)—have regarded these as concerned with smell or taste, considering that the cuticle covering the nerve-endings is sufficiently thin and delicate to permit the permeation of vapour and thus allow the nerve-endings to be stimulated chemically. Such peg-like organs are abundant on the feelers, maxillae and labium of many insects, and experiments made by Forel and others show conclusively that insects can be affected from a distance by pungent substances, the sensibility diminishing or disappearing if the feelers be cut off. N. E. McIndoo (1916), on the other hand, has pointed out the improbability of delicate chemical stimulation, such as that which results in sensations like smell or taste, acting through cuticle even though it be thin and delicate; therefore he regards these peg-like organs as tactile like the slender and more rigid hairs or spines.

The feelers and palps of insects, however, are often provided richly with sensory nerve-endings of apparently another type, which have been described by K. M. Smith (1919) as well as by several previous writers. The positions of these are evident through the presence of pits or pores on the surface of the cuticle. Study of sections of the organs

(Fig. 25) shows that the normal thick cuticle is interrupted, and that just in or beneath the aperture is a long, narrow-ended spindle-shaped cell or a group (*s*) of such cells; often delicate processes (*p*) from the cells project towards the



FIG. 25.—Section through Feeler of Syrphid Fly (*Volucella bombylans*), showing cuticle (*c*) with pore (*a*) leading to sense-organ consisting of processes (*p*) arising from sensory cells (*s*) of the skin or epidermis (*e*). *n*, nerve to brain.  $\times 600$ . After K. M. Smith (*Proc. Zool. Soc.* 1919).

pore, and these may possibly be exposed to the outer atmosphere, though they do not protrude through the pore so as to be liable to contact with external solid objects. Such nerve-endings are not tactile, but they are adapted to receive chemical stimulation by vapour diffused through the air from some odoriferous substance in food-material or in the body of another insect, or from minute floating particles. In many, if not all, of these sensory pits, however, the nerve-endings are covered by extremely thin and delicate cuticle, through which odoriferous or tasty sub-

stances might readily be absorbed if dissolved in the fluid secreted by the glandular cells said to be often associated with these organs (A. Berlese, 1909). Nerve-endings of closely similar form and arrangement to those of the sensory pits of insects are well known in vertebrate animals

as the organs whence start those nerve-impulses which, on arrival in the brain, result in sensations of smell or taste.

In many insects sense-organs of this type are found in large numbers on the feelers, and any increase in the complexity of those appendages renders possible an increase in the number of such olfactory nerve-endings. For example, in the male moths mentioned above, that can be attracted from a distance towards an imprisoned and concealed female, the segments of the feelers are drawn out into relatively elongate processes in which the special nerve-endings are present in large numbers. The number and arrangement of these organs enable an insect possessing them not only to appreciate the vicinity of a female of its own kind, but also to detect the line of advance along which she may be found. The sense associated with nerve-impulses starting from these organs is clearly similar to our own sense of smell, while the large number of the organs, their arrangement on the antennal processes, and the mobility of the feelers all combine to give distinct indication as to the direction of the source whence comes the odorous vapour. Many beetles have the segments of the terminal region of the feeler thickened or greatly expanded and flattened, so that the feeler becomes clubbed (clavate) or plate-like (lamellate) in form. The surface provided by the enlargement of these segments are the seat of large numbers of sense-organs of this olfactory type. The males of such beetles often have antennal structures more elaborate than those of the females, and their highly developed sense of smell facilitates their detection of possible mates. But in both sexes of these insects the olfactory sense serves as a guide to their food which consists commonly of strongly smelling material such as dung or decaying flesh, on which substances the females also lay their eggs.

Similar sensory pores are also found abundantly on the mouth parts of various insects, such as the maxillary palps, the epipharynx, the tip of the labium, or in some cases the mandibles. These have usually been regarded as organs of taste, as by F. Will (1885), A. Forel (1908), and other



students. N. E. McIndoo (1916) has, however, given some reasons for doubting whether the so-called gustatory sense of insects can really be distinguished from their sense of smell. Such discussions illustrate the uncertainty which must surround our conceptions of an insect's conscious sensations, and indeed many physiologists regard our own discrimination of flavours as referable to smell rather than to taste. But there can be no doubt that the minute structure of sense-organs of this type indicates clearly that they are adapted for receiving chemical stimuli such as those which give rise to normal sensations of smell and taste, and there are many recorded experiments and observations on the reactions of various insects which afford support to this opinion.

On several occasions A. Forel (see 1908, pp. 73 f.) performed experiments which appear to prove the presence of definite olfactory nerve-endings in insects' feelers. Ants recognise members of their own communities by smell, and as they approach one another their feelers are constantly moving; when these appendages are removed ants were found to distinguish no longer between sisters and strangers. Female flies of the bluebottle group lay their eggs on the flesh of dead animals, and there is no doubt that the approach to a carcase for the purpose of egg-laying is a reaction to the olfactory sense. Forel found that if the feelers of such flies be removed they lose the power of locating the objects on which they lay their eggs, while a fly, thus mutilated, and actually placed on a putrid mole did not at once lay eggs thereon as a normal female would have done. From such results it appears that the approach to a suitable breeding place, and the laying of the eggs thereon, are alike actions reflex to the reception of olfactory stimulation. Burying beetles (*Silphidae*) not only lay their eggs on dead animals, but themselves feed on such carrion. In these beetles the terminal segments of the feelers are thickened so as to form a club, and the removal of the clubbed tips of the feelers rendered the beetles incapable of finding their food and breeding-material. Further, a male Silkworm Moth (*Bombyx*



*mori*) failed to find its mate when deprived of its feathered feelers, though in its normal state it would run from a considerable distance straight towards a female across the floor of a room.

That many insects are able to discriminate between foods of various composition has been shown by several observers and experimenters, whether the sense by which the differences are appreciated be defined as taste or smell. McIndoo (1916) describes the result of mixing various substances with honey or candy offered as food to bees. While as many as 35 or 40 out of a hundred bees ate the pure sweetmeat, none would take candy to which oil of peppermint or carbolic acid had been added, though 22 per cent. partook of honey contaminated with whisky and 29 per cent. were attracted by cane sugar with a small amount of cider vinegar. When the bees were offered the alternatives of pure cane sugar, cane sugar and quinine, or cane sugar and strychnine, 47 per cent. ate the first, nearly 6 per cent. the second, and 4.6 per cent. the third; but when the only alternative was between the sugar treated either with quinine or strychnine, 49 per cent. showed preference for the quinine flavour while only 4 per cent. would take the strychnine. The experimenter was especially impressed by this last result, as he failed himself to distinguish by tasting between quinine and strychnine. Pure cane sugar was markedly preferred to sugar containing various salts of sodium and potassium. No bees would eat sugar and potassium cyanide, but sugar and potassium ferrocyanide attracted 33 out of a hundred bees to whom nothing else was offered to eat.

Reference has been made to the precision of movement which most insects display whether they creep, walk, run, or fly, and observers of their movements have often inferred that they possess some kind of sense of direction. In many cases the adjustment of motion to direction may be most reasonably supposed to work through vision, but many facts suggest that insects possess a definite equilibrating sense analogous to that which is associated with the semi-

circular canals of a vertebrate's ear, the motions of the insect being responses to nerve-impulses that result from its position with respect to a plane vertical to the surface of the earth.

Insects belonging to the large order of the Diptera or two-winged flies have the hindwings reduced to small drum-stick like rods known as halteres. Many experimenters have shown that if one or both of these organs be cut away from a fly's thorax, the insect is no longer able properly to control its flight. Microscopical investigation of the base of the halteres made by B. T. Lowne (1890) and others shows that they contain numbers of the remarkable sensory structures which have been observed and described by V. Graber (1882) and many subsequent observers, in various parts of insects of diverse orders, and called chordotonal organs. We may therefore regard it as highly probable that the function of some chordotonal organs at least is to receive impressions from the movements of the surrounding blood which lead to "equilibrating" sensation when passed on to the central nervous system. Recent investigations into the minute structure of these organs by W. N. Hess (1917) have shown that they consist essentially of elongate spindle-shaped sense-cells whose axes are prolonged as afferent fibres while their distal ends are in contact with peg-like scolopales enveloped by accessory cells, the whole organ surrounded by a delicate outer sheath (Fig. 26). The tips of the scolopales are surrounded by cover-cells, and these delicate sensory endings may either float freely in the blood-spaces of the insect's body or be connected by a terminal ligament with some part of the cuticle (Fig. 26, A, I). In either case the direction and pressure of the surrounding fluid in contact with the chordotonal organ will vary according to the position of the insect's body in relation to the horizontal and vertical planes, so that such organs afford the necessary mechanism for inducing equilibrating sensations.

But chordotonal organs have generally been regarded as connected with the sense of hearing, and there can be no

doubt that in many cases of their occurrence this belief is well-founded, because they are associated with some

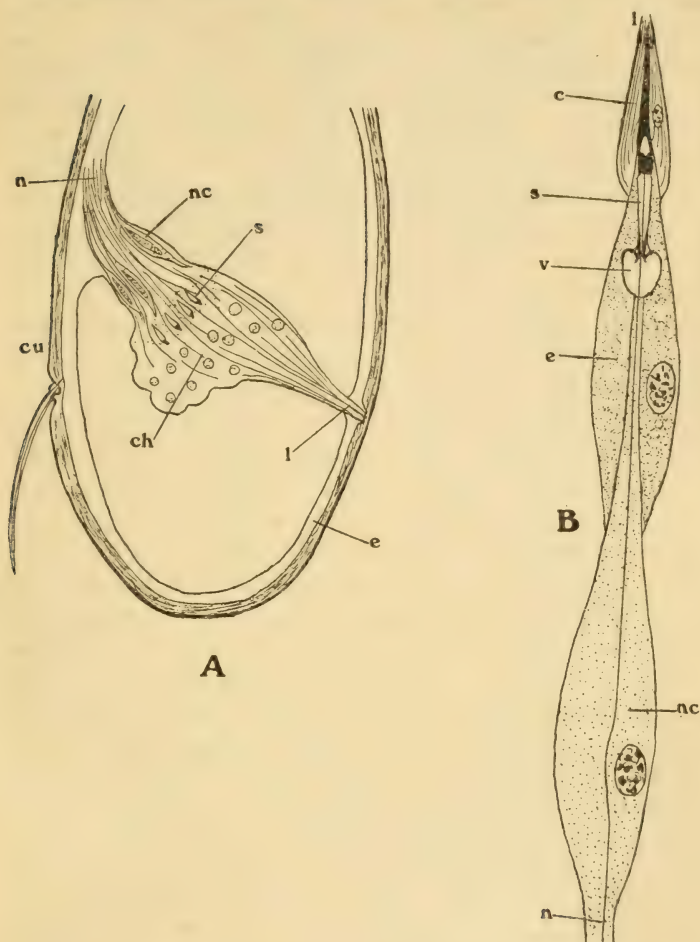


FIG. 26.—A, Cross-section of hind shin of Red Ant (*Myrmica rubra*) showing chordotonal organ (*ch*) with its scolopales (*s*), ganglion cells (*nc*) and nerve-fibres (*n*). *e*, epidermis; *cu*, cuticle.  $\times 120$ . After C. Janet ("Observations sur les Fourmis," 1904). B, Scolophore from the chordotonal organ of a Longhorn Beetle Larva (*Ergates*). *l*, ligament; *c*, cap-cell; *s*, scolopale; *v*, vacuole; *e*, enveloping cell; *nc*, ganglion cell; *n*, nerve-fibre.  $\times 500$ . After W. N. Hess (*Ann. Entom. Soc. Amer.* x, 1917).



specialised region of the cuticle, thin, tense and delicate, evidently serving as an "ear-drum" which can be thrown into vibration by sound-waves impinging on it. Further, it is to be noted that in most kinds of insects which possess such auditory organs, there are found also special structures for producing sounds. The best known of insect ears are probably those found on the first abdominal segment in ordinary grasshoppers and locusts. On either side of this segment in a locust the sub-circular or ovoid membranous ear-drum is easily seen without the help of a magnifier; close in front of it is the spiracle of the segment, and over the lower area of its inner surface are spread the fibres of the tensor muscle whose contraction increases its tightness. Attached to the inner face of the drum-membrane, near its centre, is a nerve ganglion in connection with the auditory nerve going to the central system. This ganglion, often called Müller's organ from its discoverer of a century ago (Johannes Müller, 1826), contains a number of large nerve-cells, which receive impulses from groups of chordotonal organs, whose distal ends are bound to the drum membrane, and transmit the impulses through the fibres of the auditory nerve to the segmental ganglia of the ventral trunk-cord.

These remarkable "ears" on the abdomen in grasshoppers and locusts are among the best known of insect sense-organs. Only recently, however, have we become acquainted with ears of a somewhat similar nature on the abdomen in certain moths of the Geometridae, Uraniidae, and allied families, and on the thorax of Noctuidae, Arctiidae and their allies, mainly through the researches of F. Eggers (1919) and H. Eltringham (1923). The tympanal organs of a geometrid or uraniid (Fig. 27) belong to the second abdominal segment, not the first as in a locust. The cuticle of this segment is inpushed on either side to form a hollow vesicle, often much shallower in the male than in the female moth, and at the front aspect of this vesicle the delicate ovate drum-membrane (*t*) is evident. Connected with the strong ridge surrounding the tympanic membrane are radiating bands of muscle fibres serving apparently to regulate the

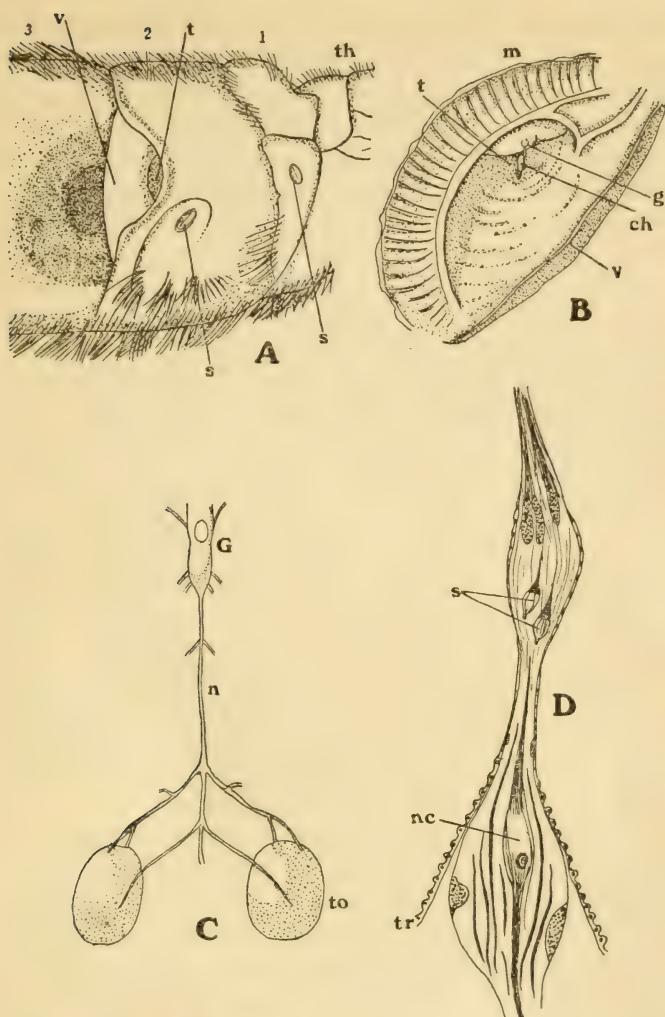


FIG. 27.—A, Lateral view of metathorax (*th*) and the first three abdominal segments (1, 2, 3) of male Uraniid moth (*Chrysiridia ripheus*), scale-pad removed to expose vesicle (*v*) and tympanum (*t*) of ear; *s*, spiracles.  $\times 6$ . B, Internal view of tympanum (*t*), with muscle bands (*m*), chordotonal organ (*ch*) and ganglion (*g*); *v*, cut edge of vesicle.  $\times 20$ . C, Thoracic ganglion (*G*) and nerve-cord (*n*) with branches to tympanal organs (*to*).  $\times 8$ . D, Chordotonal organ of female, with scolopales (*s*), ganglion cells (*nc*) and tracheal sheath (*tr*).  $\times 400$ . After H. Eltringham (*Trans. Entom. Soc.* 1919).

tension of the membrane, the inner surface of which, formed by a modified air-tube, is in touch with a ganglion and tympanic thread surrounded by a sheet of tissue derived from the air-tube system and containing scolopales characteristic of chordotonal organs (Fig. 27). In a noctuid or other moth in which these organs are thoracic, they are present on the metathorax, or hindmost segment of that region of the body. Eltringham summarises their structure by stating that each organ "consists essentially of a modified tracheal vesicle carrying two drums. One of these is the true tympanum with its chordotonal thread and the other would seem to be a kind of resonator." The tympanum lies, according to Eggers, in a lateral and ventral position with regard to the "resonator."

The nature of these organs with their drums and nerve-cords leaves little doubt that their function is auditory, and with regard to the grasshoppers and locusts, this conclusion is supported by the well-known fact that the males of such insects produce a shrill chirping noise by rubbing certain wing-nervures over blunt pegs on their hind thighs. Noises produced by moths, though less familiar, have been detected by reliable observers; it is remarkable that the Death's-head moth (*Acherontia*) whose mouse-like squeak has often been described, belongs to a family (*Sphingidae*) in no member of which have tympanal organs been detected.

In long-horned grasshoppers and crickets it is well known that there are ears situated in the front shins, paired inpushings of cuticle below the knee-joint being in contact with an expanded air-tube, so that the vibrations can affect a set of nerve-endings arranged along an extended ridge. The organs have been well described by N. von Adelung (1892) and others, and J. Regen (1912) has shown that females of a cricket *Liogryllus campestris*, normally attracted by the chirping of the males, were no longer influenced after their auditory organs had been removed. It is possible that in many insects such organs as these may be responsive to vibrations too rapid for appreciation by means of the human ear.



There remains for consideration the sense of vision, or of some dimmer perception due to the stimulation of nerve-endings by the impact of light-rays, referred to at the opening of this chapter. An insect's eye is a sense-organ of considerable complexity, but it is, like all the various types of sense-organ, due to a modification of the skin with its overlying cuticle and the connection of certain special sensory organs in the skin with the underlying nervous system. The cuticle covering an eye may be relatively thick, but it must be transparent to allow rays of light to pass through and stimulate the nerve-endings beneath. In many insect larvae groups of small circular or sub-circular simple eyes (*ocelli*) are readily observed on either side of the head, while many adult insects have two or three ocelli on the vertex (Fig. 10, *b*). Their surface presents a glassy aspect, and the deeper structures imperfectly seen through the transparent cuticle (cornea) appear black on account of the dark pigment which is contained in or associated with the visual cells of animals generally. Microscopical examination of the simple eye or ocellus of an insect shows that the transparent cornea is convex on the upper surface, and possibly also on the lower, beneath which the living cells of the skin extend in a continuous sheet; the cornea has of necessity been formed by the activity of these cells. Below them come the receptive cells which form the retina of the eye; they are elongate and taper towards their inner ends which are produced into the axes of fibres. These retinal cells, which are derived immediately from the skin, may contain a quantity of dark pigment or the pigment may be accumulated in special cells intercalated between groups of retinal cells, the retina being thus divided into a number of small cell-groups (*retinulae*). The structure of such a simple eye suggests that the circular convex cornea acts as a lens, the rays of light converging on the sensitive retina whence nerve impulses pass on through the fibres to the brain. Eyes essentially of the same type as these insect ocelli are found also among worms, molluscs, and other animals. Further discussion of their function may be postponed until we

have described the main features of the compound eyes which are particularly characteristic of insects and of their relations the crustacea.

The pair of convex, dark compound eyes present, in most insects, a conspicuous feature of the head. Each eye may occupy a comparatively small round or oval area as in a bug or beetle, or may assume an extensive protruding sub-spherical form as in a breeze-fly or a dragon-fly.

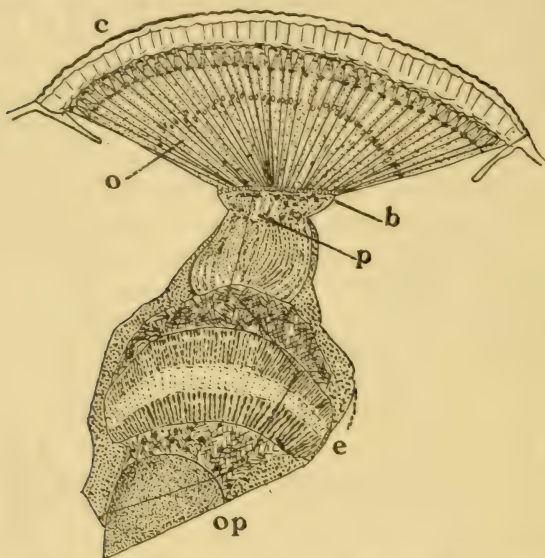


FIG. 28.—Section through Compound Eye of Honey Bee (*Apis mellifica*). *c*, cornea; *o*, ommatidia; *b*, basement membrane; *p*, perioptic; *e*, epiptic; *op*, optic.  $\times 100$ . After E. F. Phillips (*Proc. Acad. Nat. Sci. Philadelphia*, 1905).

Examining with low magnification the surface of such a compound eye it is seen to be made up of many small, usually hexagonal areas which may be numbered by hundreds or even by thousands. Examination of a section cut through the eye (Fig. 28) vertical to its surface demonstrates that the elements of which it is composed are arranged so as to converge from the inner face of the cuticle (where each element is in contact with one of the small hexagonal

areas or corneal facets) towards the underlying optic ganglion. It is therefore evident that such an eye is adapted for the transmission to the ganglion of a number of nerve impulses due to the impact of light waves from many quarters of the insect's surroundings, these impulses travelling along converging paths towards the central system, and giving rise to visual impressions from a wide range of direction. A fly with two such eyes, large and sub-globular, occupying the greater part of the surface of the head, should evidently be able to receive impressions through the eyes from before, above, and beneath as well as from either side, and to some extent from behind. While we recognise thus the great scope of an insect's vision as regards direction, we remember that the corneal area of the compound eyes, consisting of a modified portion of the head-cuticle, cannot be moved, and we realise that insect vision must differ greatly from our own and that of most vertebrate animals, in that neither both eyes nor one can be brought to bear especially on a comparatively small region of the environment, the close examination of which might be desirable. Even a superficial view of an insect's compound eye inclines us therefore to the opinion that the sight of such a creature is by no means like ours, and we may surmise that what the insect gains in range of direction it may lose in perception of distant objects as well as in clearness of definition. Before pursuing this line of discussion it will, however, be advisable to consider in some detail the structure of the elements that compose an insect's compound eye.

The eye of the well-known Honey Bee has been well described by E. F. Phillips (1905), and his account is summarised in R. E. Snodgrass's works on that insect (1910, 1925). Each corneal facet is the outer area of a thickened transparent section of the cuticle which may be regarded as a lens (Fig. 29, *cr*). Beneath each lens is a transparent crystalline cone due to the modification of four special cone-cells derived from the skin (Fig. 29, *c*). Beneath each cone is a clear rod (rhabdom, *r*) due to the modification and elongation of four other cells. Around



each rod are grouped eight elongate cells which compose the retinula (*rt*) of the element, and each retinular cell is prolonged into a fibre that perforates the inner basement

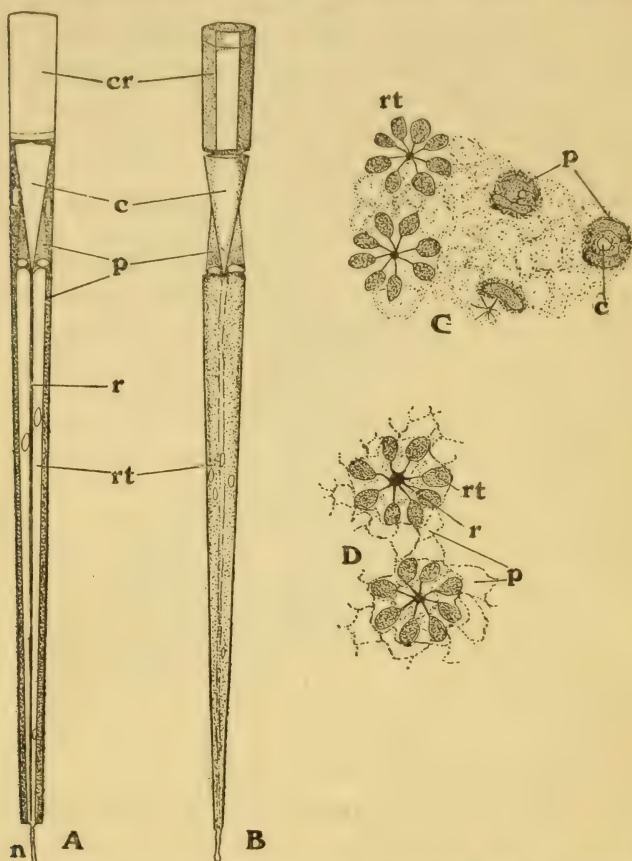


FIG. 29.—Details of Ommatidia of Compound Eye of Honey Bee, A, Longitudinal section of an ommatidium; B, Surface view; C, Oblique transverse section through apices of cones and outer region of retinulae; D, Transverse section through retinulae and rhabdoms. *cr*, corneal facet and lens; *c*, crystalline cone; *r*, rhabdom; *rt*, retinula; *p*, pigment cells; *n*, nerve-fibre. A and B  $\times 450$ . C and D  $\times 1000$ . After E. F. Phillips.

membrane of the eye and passes on towards the optic ganglion. Each series of lens, crystalline cone, rhabdom

and retinula makes up an element or *ommatidium* of the compound eye and the ommatidia (Fig. 28, *o*, 29) which correspond in number with the corneal facets, are isolated from each other by pigment cells (Fig. 29, *p*). As the ommatidia converge inwards from the surface of the eye it is evident that each of them is concerned with the reception of impressions coming along a path represented by a continuation of its axis, since rays of light not closely parallel with this axis, which pass through the lens, will be absorbed by the surrounding dark pigment. The transparent cones allow the light-rays to reach the underlying rods and thus to excite the reticular cells that surround them. From the retinulae nerve impulses pass along the fibres to the optic ganglion, through a series of cell-stations the first of which form a periopticon (Fig. 28, *p*) lying within the basement membrane of the eye, and the second an epiopticon (*e*) in the outer region of the optic ganglion. From this latter the impulses pass to the central ganglionic opticon (*op*), a mass of nerve-cells in connection with the central brain. The nerve fibres passing between the various cell-stations undergo extensive crossing-over (decussation), so that some impulses started in the upper elements of the eye pass to the lower, and those from the lower elements to the upper. Such a scheme for the reception of the impulses in the brain ensures a certain amount of co-ordination of the multitudinous impressions that affect the central nerve-masses through the two large compound eyes of a highly organised insect.

We may now pass to consider the nature of an insect's sight. The eyes are clearly adapted to receive visual impressions, but it is by no means certain that an insect sees as a vertebrate animal sees, and such questions as "Can an insect clearly discern the form of surrounding objects?" or "Can it distinguish between various colours?" have often been asked, and have been very differently answered by different students.

In the simple eyes of insects, such as the three ocelli on the crown of a bee's head, or the group of such organs on either side of the head in caterpillars and other larvae, we

have seen that the cuticle is thickened so as to form a biconvex lens beneath which lie the retinal cells. Here, therefore, is an arrangement by which rays of light coming from surrounding objects may be brought to a focus on the retina so as to produce there an inverted image. From the analogy of structure of a vertebrate's eye and our own experience of seeing, there seems no reason to doubt that an insect's ocellus is adapted for the appreciation of definite form. But in contrast to the vertebrate's eye, the ocellus has no provision for accommodation, and the usual high convexity of its lens renders it available for seeing only objects that are close at hand, while the extent of its field of vision must be greatly restricted.

A compound eye consists of a number of elements each consisting of a set of transparent structures—cornea, lens, cone, rhabdom—the last-named surrounded by the receptive reticular cells connected by fibres with the ganglionic centre towards which the closely arrayed elements converge. J. Müller long ago (1826) pointed out that the general visual sensation induced through such an eye must be regarded as the sum of the multitudinous sensations due to the individual elements which, owing to the surrounding dark pigment are more or less insulated from one another. Such a hypothetical "built up" impression suggested to Müller the term "mosaic vision" from the analogy of a picture made up of a number of small apposed pieces; and this term has been generally accepted as being suitably descriptive of an insect's seeing with its compound eyes. But how far is such vision definite? Müller denied that any clear image could be formed in a compound eye and suggested that an insect receives no more than the impression of as many spots of light as there are elements, the slender pencil of rays traversing each element being concentrated at the apex of the cone and the intensity of light appreciated through each element varying with the source whence it comes.

H. Grenacher (1879) recognised that the lens of each element is adapted for the production of an image, but believed that the position of the image is such as to render



impossible its appreciation by the reticular cells. Recently, however, good reason for regarding compound eyes as capable of appreciating a distinct image has been given in an extensive study of the subject by S. Exner (1891). His work has been well expounded by H. Eltringham (1919) who by observations and experiments of his own has carried it farther. Exner describes how in the common glowworm—the wingless larva-like female of the beetle *Lampyrus noctiluca*, an insect active in feeble light—the pigment cells may move outwards towards the corneal surface, so that the deeper regions of the elements are no longer completely isolated, and some of the rays traversing a cone may affect not only its own retinula but also neighbouring retinulae. The result is the formation of a set of erect images partly superimposed on each other, and it follows that the glow-worm may thus obtain clear and definite vision of a portion of its near surroundings. These superposition images are believed by Exner to be characteristic of the vision of those insects, such as moths, which fly in the dusk or at night time and have therefore to make the best use of feeble light. Eltringham has studied the images formed by the eyes of day-flying insects such as butterflies, dragonflies, and blue-bottles. In the case of the two latter groups, in which the cone-forming cells are imperfectly changed into the completely “crystalline” substance, he agrees with Exner that the general apposition image induced may be best represented to our imagination as “a mosaic of light spots.” But in the compound eyes of butterflies which possess fully developed transparent cones, “there is at the apex of the cone a tiny erect image of that part of the field appertaining to each facet unit.” Hence it may be inferred that an erect image of the whole field of vision may be appreciated by means of such an “eucone” eye. The reinversion of the images by the cone, so as to make them ultimately erect, disposes of the difficulty arising from the conception of an extensive general image, made up of a large number of minute individual images each regarded as reversed.

But the clarity of an insect's vision as regards form is

presumably less than that of a vertebrate's because the retinal structure of an insect's eye is distinctly coarser. And it has already been mentioned that the lack of any provision for accommodation results in the insect being very short-sighted. "We know," remarks Eltringham, "how readily one white butterfly will pursue and investigate another to see if it is a suitable mate, but I have never seen this kind of flirtation begin from a distance of more than a few feet." The compound eyes of insects, therefore, while giving their possessors a wide range of vision as regards direction, are ineffectual in perceiving objects at a distance, and in some cases only can they receive from objects close at hand any definite indications of form.

A subject of great interest in connection with the sight of insects is their appreciation of colour. Information as to this cannot be obtained by microscopic examination of the eye structure, but approximate certainty has been reached by means of careful observations and experiments. Reference has been made above to the fact that a butterfly often pursues one of its own species; such action is due to visual recognition, because the attraction is also exercised by a dead dried specimen or even by a coloured model, as Eltringham has demonstrated. He found that a common "fritillary" (*Brenthis euphrosyne*) dipped directly to a spot on the ground where was lying a wing accidentally broken off from an insect of its own kind long dead. This observation affords convincing evidence that the butterfly could recognise the characteristic colour of the wing, for any specific scent must have been for a long period absent from such a dried fragment. Many investigators have concluded that insects of various kinds distinguish the colours of flowers on account of the apparent preference which they show for certain hues. Eltringham watching Vanessid butterflies on a bed of asters, white, pink, and purple, found that of 427 visits, 47 were to white, 135 to pink, and 245 to purple flowers, though the purple blossoms were only three-quarters as many as the pink. H. Müller (1878) was long ago led to the opinion that the colours of flowers serve as

an attraction to insects that visit the blossoms to obtain nectar, and the doubts that some subsequent observers have thrown on the existence of a true colour sense in insects do not seem to be justified. An experiment of J. Lubbock (1882) often quoted, and several times subsequently verified, is especially valuable in this connection. He placed honey on a coloured paper disc and thus trained bees to associate a particular colour (red or blue, for example) with the location of food ; then he found that a bee which had once found honey on a blue disc would return to a disc of that colour even though the food were now not on a blue but on a red one. This experiment shows that in such cases the attraction by colour must be more powerful than the attraction by scent, and confirmation has been afforded by Forel and others who, having varnished or removed the feelers of various insects, found that reaction to the colour stimulus remained unaffected.

We may conclude, therefore, that the eyes of many insects enable the creatures to distinguish the forms and colours of near objects ; Eltringham estimates that butterflies recognise members of their own species when about a yard away. Those with large compound eyes can see in many directions at once. Beyond the restricted distance for which the lenses and cones of its eyes afford suitable focus, an insect can appreciate changes in the intensity of the light falling on its corneal area. Any one who passes his hand above the station of a resting fly can demonstrate that an insect perceives a moving shadow, readily if the motion be rapid, less distinctly if it be slow. If the observer is trying to catch the fly with his moving hand, he may go farther in his interpretation of the insect's behaviour, and conclude that the approaching shadow "startles" or "frightens" it when he sees it dart suddenly away.

This reference to the possible sensations or mental experiences of insects recalls the opening remarks of this chapter on an insect's response to stimulation from a source of light, and the inferences that may be drawn from the creature's behaviour. It may be advisable to return to such



questions before bringing this section of our study to a close.

Many insects, like the proverbial moth, fly directly towards a lamp, and the observations of J. Loeb (1905) and others show that a definite relation of the creature's body axis to the source of light is always brought about. The light seems, one may say, to exert a pull on the insect, inciting it first to turn head on towards the light, and then to move its body as a whole along the path of the luminous rays in the direction opposite to their course, so that at length it flies against the lamp. Such a response is usually called a tropism, because the insect is inevitably turned in a certain direction and along a certain path under the impact of the stimulus. As this response draws the insect towards the source of light it is defined as "positively phototropic." The same reaction is shown by many larvae as well as by winged insects. Caterpillars commonly move towards the light. "If they are obliquely placed," writes E. L. Bouvier (1922), "on a plane surface opposite to the source of light they quickly turn their heads, following the axis of the light ray and then the rest of the body moves in this direction." On the other hand, there are insects on which the influence of light is the exact reverse of this; they turn away from it, as may be observed by W. B. Hearn (1911) in the maggots of flies or bluebottles exposed to bright daylight or strong lamp-light. These larvae first direct their heads from the source of light and then move away towards the gloom. So experimenters call them "negatively phototropic." It is important to realise that such terms as these, while convenient for analytical definitions of behaviour, offer no explanation of such behaviour; they simply express in two or three long words that some insects appear to seek and others to shun the light. But the use of the word tropism to define such responses of insects to stimulus is generally taken to imply that the response is automatic and not necessarily accompanied by any distinct sensation or experience; the term was long ago applied to describe the behaviour of plants in response to luminous and other

stimulation from their surroundings, and nobody has seriously suggested that the growth of a plant shoot towards the light is accompanied by sensation in the organism. According to Loeb's interpretation of phototropic reaction, the incidence of light on one side of the sensitive head region of the insect leads to a corresponding one-sided action of the body-muscles so that the creature is necessarily turned in the direction of the rays of light. Then the "luminous intensity being the same on both sides, there is no reason for the animal to turn from this direction either to the right or to the left." It must now directly approach or recede from the source of light. It is noteworthy that the fly-maggots taken as examples of negative phototropism have no eyes, and there is no reason for attributing any definite visual sensation to them. But insects like moths that fly into a lamp have eyes, and even though their reaction to the light be automatic and inevitable, it does not necessarily follow that they have no appreciation of the light towards which they are irresistibly drawn. The apparently suicidal action of a moth flying at last into a flame may be due to the "pull" of the light in rapid alternation on either side as at close quarters the insect turns to and fro.

Other responses to stimulation mentioned in this chapter may be recognised as referable to the group of tropic actions. The male moth "allured" by the caged female, or the female fly attracted by carrion to her egg-laying, is positively chemotropic, while the black aphids which climb as high as possible on the bean-shoots where they feed are negatively geotropic; they turn from the earth with its gravitational attraction. The consideration of these and similar actions leads naturally to the wide subject of behaviour.

## CHAPTER V

### BEHAVIOUR, INSTINCTIVE AND INTELLIGENT

IN the preceding chapter our consideration of the sense-organs of insects and the reactions associated with their working has led to comparisons between the sensations and responses of insects and those of back-boned creatures, including our own race. The behaviour of insects—especially of those groups which exhibit a highly developed family or social life—has been repeatedly used by earnest teachers of mankind to stimulate their fellows to more strenuous habits of life and work. “Go to the ant, thou sluggard ; consider her ways and be wise ” was the call of the Hebrew seeker after wisdom to the men of his day, and such calls have been echoed since through the ages. Survivors from the nineteenth century remember how in their youth they were “exhorted to virtue” in the verse of Isaac Watts :—

“ How doth the little busy bee  
Improve each shining hour,  
And gather honey all the day  
From every opening flower ! ”

But some years before that century closed F. Anstey had suggested that the “modern child” of the period might be expected to reply to such exhortation in this wise :—

“ How doth the little bee do this ?  
Why, by an instinct blind.  
Cease then to praise good works of such  
An automatic kind.”

We will return to the specialised activities of ants and bees in a later chapter ; the points of view contrasted in the two verses just quoted are, however, among those



applicable, in the opinion of different students, to the behaviour of insects generally, and indeed to that of animals lower or higher in the scale of life than they. Already comment has been made on the tendency to credit insects, when they show response to stimulation of various kinds, not only with sensations but with states of consciousness—pleasure, discomfort, terror—comparable to those which we realise in our own experience. The food-gathering activities of ants and bees look like conscious efforts directed intelligently to an obvious purpose. That is the assumption underlying the belief that such insects display industry and foresight in their work. On the other hand, Anstey's verse suggests that the purposeful activities of insects may be carried on without design or knowledge on their part, and such an outlook on the subject has become increasingly popular during recent years. It is undeniable that a large proportion of the actions of insects are reflexes resulting directly from various stimulations from outside, which call forth inevitable responses through the nervous system of the insect acting on its muscles. The term "instinct," often used somewhat loosely to describe the causes of actions not due to intelligence on the part of the agent, has at its root the idea of "need" or "urge." But such urge or impulse arises as the response of the organism to stimulation, and instinct was therefore defined by Herbert Spencer as "compound reflex action," and a creature's instinctive behaviour has been regarded as the sum of its responses to environmental influence. Stimulations are being continually received by means of the various sense-organs, and the insect's nervous system is of such a nature that certain responses follow in each case. The simplest form of response is some kind of tropism such as was described at the close of the previous chapter (pp. 92-3), and some recent distinguished students of insect behaviour—A. Bethe (1898) and J. Loeb (1905), for example—believed that all the life-activities of the creatures can be explained as a complex of tropisms. Light, gravity, contact with particles of soil, odorous plant secretions, all affect the insect and the

result in each case follows certainly, so that the behaviour of a bee among blossoms may on this interpretation be strictly compared to "the behaviour of iron filings in the magnetic field." On this view the observable actions of an insect depend altogether upon the kinds of stimulation to which it may be subjected, along with the innate tendency of its tissues and organs to respond to such stimulations in particular ways. A moth flies into the candle flame that destroys its life, because it must needs react to a source of light by way of direct approach. And on the other hand, a female housefly makes for a heap of refuse and lays her eggs therein, because the smell of the refuse is an attraction, and the nerve impulses pass on to the centres that control the actions of the genital ducts and ovipositor, so that the laying of eggs is part of the bundle of reflexes, which in this case leads not to the curtailment of the insect's life but to the perpetuation of its race. Such insect activities as can be explained by this simple "tropic" formula may therefore be either harmful or beneficial to the species. What impresses the thoughtful observer is that if strikingly adaptive actions are the result of simple reflexes, there remains the further question why the combined reflexes work out to a beneficial end? While the study of tropisms undoubtedly helps the naturalist to analyse the activities of insects, it appears that the explanation of all kinds of insect behaviour as due to these reactions may be deceptively simple. The observer who attributes to an insect motives and states of consciousness like his own, because he sees a moth fly towards a lamp or an ant scuttle into a burrow, is misled by false analogies of behaviour. But such an observer at least recognises that the insect that he watches is alive, while the rigid follower of the tropic explanation, who is certain that all the creature's actions are inevitably determined by the nature of the stimulations from without that affect its nervous system or act directly on its various tissues, seems to overlook those stimulations which may originate within the organism and give rise to aspects of behaviour unforeseen and inexplicable.

Some recent experimental work by D. E. Minnich (1919) on the reaction of Hive-bees (*Apis mellifica*) is of importance

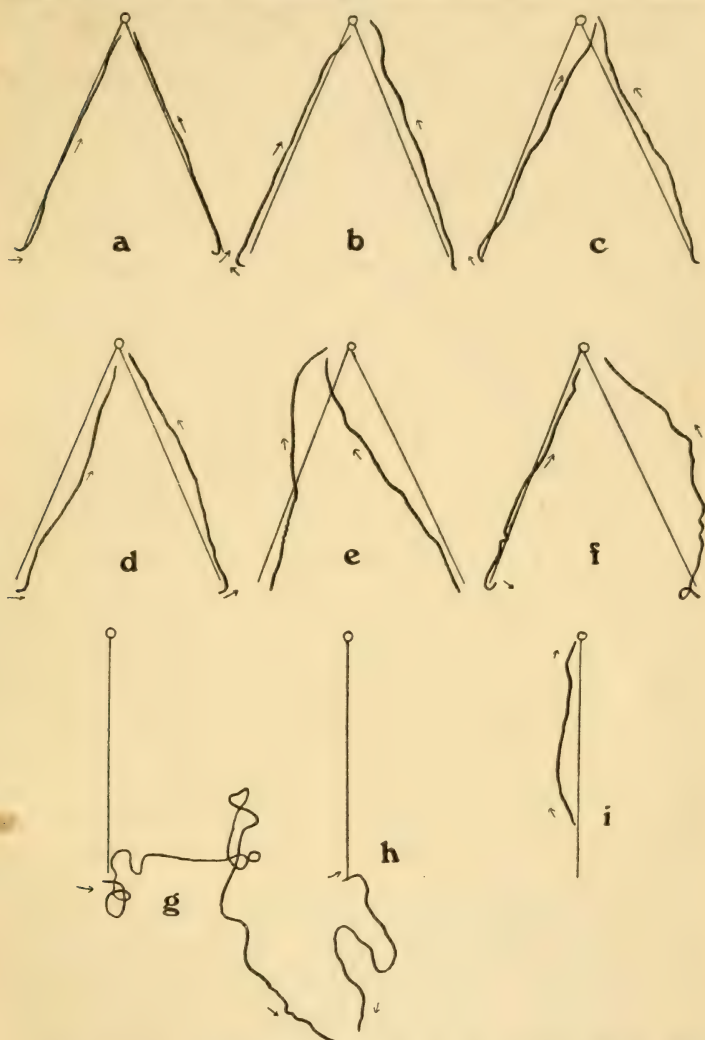


FIG. 30.—a-f. Two trails of each of six normal Honey Bees (*Apis*) in directive light. g, h, i, three successive records of trail of another normal bee in directive light, the first two (g and h) being altogether contrary to expectation. After D. E. Minnich (*Journ. Exper. Zool.* xxix, 1919).



in this connection. Bees are markedly phototropic, stimulated by light, flying or crawling towards a definite source of illumination. Minnich shows, however, that individual variations may be apparent in their responses. Bees generally turned rapidly so as to face, then crawled towards, a "directive" light, but only about a quarter of the number whose course was carefully traced, made for the lamp in an approximately straight line, the rest showed more or less deviation, and in a few cases the path was markedly indirect. Out of seven bees tested on one occasion, six responded by making directly for the source of light (Fig. 30, *a-f*). The seventh on its first trial wandered around and away; fourteen minutes later it went by a less circuitous route away from the light; but a minute later, starting from a point 30 cm. nearer to the lamp, it made for it though not in a straight line (Fig. 30, *g, h, i*). "This example shows," comments Minnich, "that even the constant response of the bee to directive illumination is not free from abrupt and apparently inexplicable departures." Experiments with bees allowed to wander in a uniformly illuminated area ("non-directive light") demonstrated much variation in their individual behaviour. "The animal may turn markedly towards a given side in one trial, and in the next turn quite as markedly towards the opposite side. Again, the direction of turning may be completely changed several times in the course of a single trial." It seems clear, therefore, that the reaction of at least some hive-bees to visual stimulation is not so fixed as to be absolutely predictable. The bee may convince the observer that she is alive by behaving sometimes in an unexpected manner.

A set of experiments performed by Minnich on bees with one eye blackened over so as to be impervious to light or almost so, is of very special interest. Many observers have tried similar experiments with various insects, and find that their reaction to directive light is to "loop" towards the side on which the eye is still functional. Minnich showed that some of the bees subjected to such treatment learned by experience to modify this reaction so that their

course came to approach that of a normal bee with both eyes in use (Fig. 31). Through a number of trials some of these insects were observed gradually to reduce the number

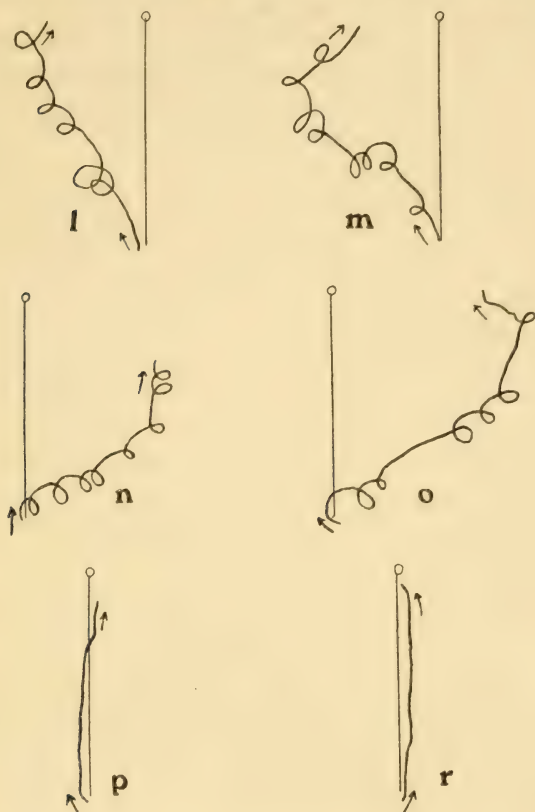


FIG. 31.—*l, m*, two trails of a Honey Bee with right eye obscured ; *n, o*, two trails of a Bee with left eye obscured, showing tendency to turn constantly towards the side of the functional eye. *p, r*, two trails of a Bee with left eye obscured, which behaved as a normal insect approaching the source of light. After D. E. Minnich (*Journ. Exper. Zool.* xxix, 1919).

In Figs. 30 and 31 the small circle represents the source of light and the thin straight line the direction of the rays.

and frequency of their "circus" movements, until after twelve or twenty trials, they made for the source of light in

an approximately straight line, as normal bees would do. It is noteworthy, on the other hand, that some of the bees used in these experiments never seemed able to modify their response from that at first incited through their "one-eyed" condition; they were far less ready than others to learn by experience, more completely dominated than their fellows by the abnormal reflex arising from their abnormal condition. Reference has been made to the definition of instinct as "compound reflex action," and Lloyd Morgan in his classical discussion on *Animal Behaviour* (1900) remarks that "instinct supplies an outline sketch of behaviour to which experience adds colour and shading." In the changed behaviour of Minnich's bees we have an example of the modification of a simple "instinctive" response through experience acquired by certain individuals subjected to unusual conditions in the course of their lives. The fact that some creatures become more easily adapted than others to new and strange conditions suggests the possibility of our learning a little as to the origin of new modes of behaviour among insects from such methods of investigation.

These results further lead us to conclude that an insect may be able to escape from the domination of an abnormal tropism which prevents or retards the creature's normal response to a stimulation. A bee with both eyes in action directs the axis of its body towards, and then moves towards a source of light, whereas a bee with the left eye blinded loops towards the right under the stimulation of a bright light. The fact that it may learn how to correct this abnormal reflex and revert to its former mode of behaviour suggests that in performing the normal reflex action the insect experiences at least a gleam of consciousness akin to the satisfaction which we realise in ourselves as we perform many normal reflexes, and which we may infer is realised to some extent at least by the higher vertebrates generally.

With insects, however, it can hardly be doubted that the consciousness accompanying reflexes of this kind is weaker by far than with vertebrates; the "works" of the "little



busy bee " are indeed mostly " of an automatic kind." The segmentation of the central nervous system in insects is a structural feature which suggests imperfect integration of nerve-action, and consequent imperfect individuality, and observations following mutilation, whether deliberate or accidental, convince us that there is considerable exercise of independence between various parts of an insect's body. In a trisected wasp, for example, the jaws and mouth continue to feed and the thorax to walk, while stimulation of the abdomen by a careless observer may lead to unpleasant demonstration that the sting will act as the result of a reflex conducted through the abdominal nerve-centres without possibility of reference to the brain.

Insects of various orders have the habit known generally as " death-shamming "; when touched or handled they lie motionless on the back with the limbs strongly flexed. This is a reaction to contact with certain objects, whereof a human hand is one. H. H. P. and H. C. Severin (1911), who have carefully studied such reactions in aquatic bugs (*Nepa* and *Zaitha*), conclude that the contact-stimulus works so as to bring the muscles into a state of intense contraction—a kind of prolonged tetanus. "*Nepa*, while feigning death, may be taken by any tibia or femur and held in a position so that the weight of the entire body is borne by the extensor muscles of a single segment of one leg." Here the head nerve-centres appear to exercise an inhibitory power over the muscles while the reaction lasts, for if a death-feigning *Nepa* be beheaded, the muscles immediately relax, while if the insect be bisected across the thorax the limbs in front of the cut remain flexed while those behind it relax. This term " death-shamming " has been commonly applied to this habit because it has often been regarded as a voluntary and purposeful method of behaviour adopted by the insect in the presence of some recognised danger with the object of securing safety. There seems no reason, however, for regarding it as anything beyond a simple automatic reflex, which may in some cases serve as a protection to the creature that adopts it.

No doubt can be felt that a very large proportion of an insect's normal activities are instinctive, in that they result from a set of complicated reflexes, while they serve to ensure the survival either of the individual or of the race. This is especially evident in modes of behaviour concerned with reproduction and growth among insects whose manner of life when adult differs from that in the early stages of their life-history. The actions that accompany egg-laying by a female moth or digging-wasp, for example, are all directed towards the provision of environment and food suitable for the larva. The moth, herself a feeder on the nectar of flowers which she sucks, lays her eggs on the leaf of a plant—often of some one definite species—which the caterpillar will devour. Either the plant provides a stimulus to egg-laying through the senses of smell or sight and the act is instinctive, or the moth remembers how she fed when she was a caterpillar and provides for her young accordingly. No student of insect behaviour would seriously suggest the second alternative as probable, and we feel compelled to accept the first. A digging-wasp makes a nest, usually by excavating a pit in the ground, and either before or after this labour, hunts for prey to bury along with her eggs so as to ensure a supply of food for her grubs. In most cases that have been carefully observed, the behaviour of the mother insect is so uniform that she may be said to follow a definite routine, each step in the process apparently suggesting the next, so that nothing is done out of its regular order. Some observations of G. W. and E. G. Peckham (1898) are of great interest in this connection. Some American species of *Pompilus*, studied by them, capture spiders to serve as food for the grubs; the female wasp paralyses the spider with her sting, then places it with its waist in the fork of a plant-shoot, so that it will not fall, and then proceeds to dig the hole for her nest. Wishing to observe carefully how the wasp stings the spider, the Peckhams on one occasion removed from its place on a bean plant the paralysed spider which a female *Pompilus* had just put there, and substituted an uninjured spider. The

wasp, after digging her nest, returned to the bean-plant in search of the paralysed prey, saw the uninjured substitute, but would not touch it. After several fruitless searches, the wasp went away, caught and stung another spider, placed it in the usual position on the bean-plant, and then dug another nest, although the first made one was ready and empty. The break made in the insect's usual routine by the observer's act, resulted in the whole process being started again from the beginning. Apparently the wasp recognised that the spider she found had not been stung, but she did not attempt to deal with a normal spider already in place on the plant, she was impelled to go and hunt for another. Then having stung this, she proceeded to the usual next step of digging a nest ; the available empty nest that she had made shortly before was neglected because the work of nest-making always follows, in the instinctive cycle, the stinging of the prey. The hitch in the work due to the removal of the first victim led to a repetition of the whole process from the start ; the wasp showed no adaptability to unusual conditions by making a change in the usual sequence of her actions. Her nervous system appears to be so attuned to the various stimulations and experiences that each of them, as it is felt or completed, becomes an incitement to the " doing of the next thing."

Yet these facts are no justification for denying that the insect may be a conscious being, even though its consciousness be dim and feeble as compared with that of a vertebrate. It is reasonable to believe that the insect's instinctive routine has, to quote Lloyd Morgan, " a psychological aspect of awareness and desire." Though the " outline sketch of behaviour " which is drawn, as it were, for the insect by its long-inherited instinct, is rigid and unvarying, there may be opportunity, at least in some instances, for the addition by experience of " colour and shading," as well as clear evidence of individual memory. For example, the Peckhams described in detail the behaviour of a female pompilid wasp *Aporus fasciatus* which had captured a spider larger than herself and left it on a melon leaf while she sought a suitable



place for nest-making. "At length she went under a leaf that lay close to the ground and began to dig." The observers removed the leaf so as to watch the wasp's actions more closely; after ten minutes she flew away to where she had left the spider, and then returned to seek the unfinished nest, but "it was evident that some landmark was missing—when she reached the spot she did not recognise it. At last we laid the leaf back in its place over the opening, when she at once went in and resumed her work, keeping at it steadily for ten minutes longer." But this nest was never finished; if we may judge from the wasp's behaviour its position did not satisfy her, for she filled it up and started four others in succession, each to be in its turn abandoned and filled up. At the sixth trial the nest was completed and the spider dragged in. Lloyd Morgan is justified in his comment on this description "that it shows an amount of apparent fastidiousness which is quite irreconcilable with the hypothesis that the behaviour is merely instinctive." It shows also that the wasp recognised the position of her first nest by the leaf lying over its mouth; her behaviour suggests inevitably that she remembered that leaf so that it served as a guide to the nest.

Somewhat similar results were obtained by C. Ferton (1905) in his observations on certain kinds of bees (two species of *Osmia*) which make their nests in empty snail-shells. After depositing honey and pollen and laying an egg, the bee closes the mouth of the shell with fragments of leaves worked up with her spittle. One species, *Osmia rufohirta*, has the habit of rolling the shell, after provisioning the nest and laying her egg, to some sheltered spot, returning to the latter with the covering of leaf-fragments. A female of this species was observed by Ferton to go and return between the place where she was leaf-gathering and the hiding-place of the shell by way of the station at which she had first found the latter; she travelled over her former tracks, a recognised path. While the bee was engaged on the journeys necessary for the completion of her task Ferton removed the shell from its hiding-place to a position

some six inches away. The *Osmia* failing to find the shell where she had left it, proceeded to hunt about until she recovered it, and then for several subsequent journeys made her flight to its new station by way of its two former resting-places. Afterwards, however, she was seen to go directly to the new station: "Little by little the images of the former places of her nest are effaced in the memory of the insect." E. L. Bouvier (1920) remarks on these observations that such insects "know how to manage things and to meet the most unexpected situations. They do not act as automata; the memory that guides them in these circumstances seems indeed from its essential characteristics to belong to the same degree of psychism as the human memory." It may be doubted, however, whether such behaviour, remarkable and instructive though it is, can be regarded as of "the same degree" as the memory of man.

Of all the unusual modes of behaviour by insects of which we have reliable record few have appealed more strongly to the imagination of naturalists than the work of the North American digging-wasp *Ammophila urnaria*, that captures, stings, and buries caterpillars as a food supply for her grubs. Most of the species of *Ammophila* dig their nests in the soil before hunting for prey to deposit in them, and a completed nest may harbour four or five paralysed caterpillars with as many *Ammophila* eggs. One of these females covers the mouth of her burrow with pellets of earth, but normally never fails to find the nest on her successive returns from the hunting. When the nest is fully stored and the eggs are all laid, the wasp finally closes up the mouth. The Peckhams (1898, pp. 6-32), who paid especial attention to the habits of these wasps, comment on the difference in behaviour shown by individual females in the work of nest-closing, some being much more careful in performing their task than others. "Of two wasps that we saw close their nests on the same day, one wedged two or three pellets into the top of the hole, kicked in a little dust, and then smoothed the surface over, finishing it all within five minutes. . . . The other worked . . . for an hour.

first filling the neck of the burrow with fine earth which was jammed down with much energy . . . and next arranging the surface of the ground with scrupulous care and sweeping every particle of dust to a distance." Finally, after unsuccessful trials with a small stone and a lump of earth, she laid a leaf over the closed mouth of her burrow. But it is another individual *Ammophila* that the Peckhams have made famous by observing how, after filling the hole with loose earth and ramming it down with her head, and continuing this process until the hole was full of soil to the ground level : " she brought a quantity of fine grains of dust to the spot and picking up a small pebble in her mandibles, used it as a hammer in pounding them down with rapid strokes, thus making this spot as hard and firm as the surrounding surface." In connection with this very remarkable incident, it is instructive to note that females of *Ammophila* sometimes bring small stones to serve as stoppers for the mouths of their burrows. The behaviour of the individuals that have been thus seen to use such stones for pounding down earth may perhaps be regarded as a further advance in the intelligent use of materials serving for nest-making, something beyond the usual habits of their kind.

Digging wasps paralyse their prey—whether spiders or caterpillars—by stinging the victims repeatedly, frequently applying the sting along the line of the ventral nerve-cord beneath the body. It has often been stated that the operation of stinging is always performed in the same way by all females of the same kind, and that it results in the paralysis of the victim, so that it cannot move, but not in its death, so that the wasp's grubs when hatched will find fresh food in a living though helpless prey. In order to bring about this result it is necessary that the wasp should sting the caterpillar accurately along the ventral nerve-cord so as to pierce the series of ganglia wherein are the nerve-centres that control the movements of the various segments. These considerations have led some enthusiastic naturalists to imagine that the wasp must have a knowledge of the anatomy of the caterpillar and of the functions of its nervous system.



The facts, as shown by the careful observations of the Peckhams, are that the part of the body where the caterpillars are stung varies with different females of the same species of wasp ; only occasionally does the wasp inflict a series of stings along the mid ventral line. Moreover, the victims found in the wasps' nests are often dead, and the wasp grubs can feed and grow if supplied with a dead or even decomposing victim. " We believe that the primary purpose of stinging is to overcome resistance and to prevent the escape of the victims, and that incidentally some of them are killed and others paralysed." Such considerations warn us that the student of insect behaviour who does not allow for individual variations in the habits of the same species may readily fall into the error of regarding all insects as utterly unconscious automatic machines, or into the opposite error of assigning to them intelligence and foresight of a degree far beyond that warranted by the facts of their behaviour.

The habits of egg-laying and providing in advance for the needs of offspring as yet unhatched, some of which have been briefly considered, are clearly to a large extent instinctive ; most details of an insect's complex behaviour directed to these ends result from her inborn tendency to respond in certain ways to suitable surroundings and stimulation. It is instructive, in this connection, to turn to some examples of behaviour in larval insects which appear to suggest prevision of the needs involved in the future final transformation into the adult form. Such prevision is of course impossible ; a highly imaginative observer might convince himself that a butterfly laying eggs knows what will happen to her offspring after hatching because she was once a caterpillar herself, but he could hardly be persuaded that a larva foresees its transformation into a winged insect, and knows the conditions, often seemingly difficult, that will have to be overcome in connection therewith. Yet numerous larvae of different orders follow specialised modes of behaviour which are related to their future needs, and thus afford striking example of the part played in the life

of insects by the sets of activities which we generally call instinctive.

It is well known that during the pupal stage which intervenes between the larval and the adult condition in the vast majority of insects, the creature remains, as a rule, quiescent and does not feed. In such a resting condition the insect needs protection, and its behaviour when nearing the close of larval life is largely concerned with this coming need. Before the moult or casting of the last larval cuticle which reveals the pupa (see Chap. VII, p. 172) the full-grown larva often spins a silken cocoon, as do the silkworm and many other moth-caterpillars, the cocoon in some species being strengthened with the larval hairs or bristles, or with foreign substances such as chips of wood or particles of soil. Such cocoons serve as shelters for the pupae resting within them. Or the larva, if it does not make a cocoon, often seeks shelter by burying itself in the ground as many hawk-moth and owl-moth caterpillars do, or by creeping beneath a loose piece of bark, like the small caterpillar of the codling-moth that has fed within a growing apple on a tree.

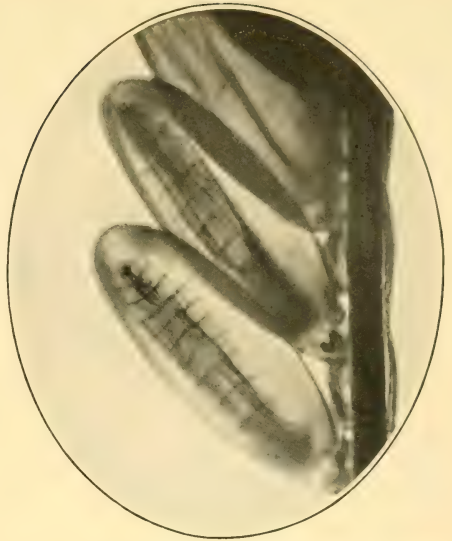
But if a pupa lies enclosed in a cocoon, the perfect winged insect, when developed, has to make its way out of the cocoon after undergoing the moult that sets it free from the pupal cuticle. Often it is found that some provision for this need also is made beforehand by the larva. The silkworm's cocoon is left comparatively thin and weak at the head end where the moth will have to come out, so that in this region it is readily weakened and partly dissolved by a fluid which the moth, when developed, discharges from its mouth. The same provision is found in the behaviour of the remarkable caterpillar of the Puss Moth (*Cerura vinula*) which forms a hard and dense cocoon, but leaves in front a weak area which is readily acted on by the strong alkaline fluid that the emerging moth discharges from its mouth, as O. H. Latter (1895) has shown.

Still more remarkable, perhaps, is the behaviour of larvae which feed in some object or substance out of which

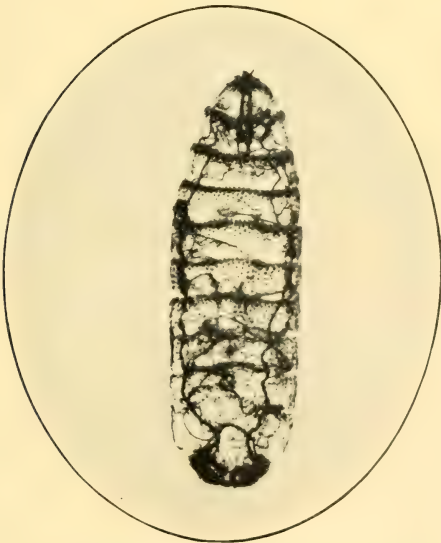
PLATE II



A. Row of Eggs on Cow's Hair  
(three are hatched).  $\times 5$ .



B. Two Eggs cleared to show unhatched Larvae.  
 $\times 45$ .



C. First-stage Larva, showing Mouth-armature  
and Air-tubes.  $\times 50$ .



D. Second-stage Larva,  
showing Muscles.  $\times 6$ .

EGGS AND LARVAE OF *Hypoderma lineatum*.

[To face p. 108.]

[T. Price, photo.]





the perfect insect has ultimately to make its way ; in such cases the larva before pupation has the habit of coming close to the surface. The large caterpillar of the Goat Moth (*Cossus*), for example, feeds for more than a year on wood as it tunnels through the timber of some tree. When fully grown it usually comes to the bark before it makes its cocoon of chips of wood fastened together by its silky secretion. This is an insect whose pupa works its way partly out of the cocoon before undergoing the final moult which releases the moth, and as the cocoon has been formed close to the surface of the tree trunk or branch, the greater part of the pupa's body projects into the air, so that there is, after that moult, no obstacle to the free emergence of the moth. The small larva of a seed-beetle (*Bruchus*), when hatched from the egg laid on a leguminous blossom, bores into the carpel and enters the developing seed, where it tunnels and feeds until fully grown. Before pupation, however, it makes its way to the circumference of the cotyledon just within the seed-coat (*testa*) where it pupates. Thence in due time the beetle emerges, though in several species of this group it may remain resting there for several months before it bites its way through the skin in preparation for egg-laying on the blossoms of the succeeding spring.

In many cases the objects within which insect larvae feed are the living bodies of other insects or of some larger animal at whose expense they carry on their parasitic existence. The modes of behaviour of insect parasites are as remarkable as their structure, and often have a definite bearing on the later stages of their own life-histories. As an example we may sketch briefly the wanderings of the maggots of the Warble-flies (*Hypoderma*) through the bodies of the cattle wherein they live. The female flies lay their eggs on the hairs of the legs or the lower parts of the bodies of grazing cattle. Immediately after hatching the tiny maggots crawl along the hair and bore into the skin. Once beneath the skin they work their way upwards, their behaviour suggesting that they have the "negatively geotropic" reaction. But their migrations are too com-

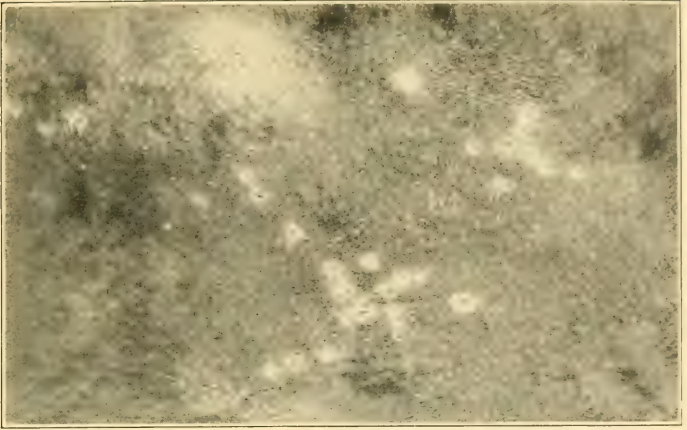
plicated to be explained as due to one tropism only, for they find their way to the sub-mucous coat of the gullet, where they rest or wander to and fro for several weeks, and whence they travel backwards by way of the dorsal muscles or the diaphragm and the vertebral canal to a position just beneath the skin of the host-animal's back. Their final resting-place is never far from the line of the beast's backbone, which suggests that negative geotropism may still be one factor governing their behaviour, and not long after their arrival there they perforate the beast's skin. This action ensures a supply of fresh air to the spiracles at the tail-end of the body directed towards the hole during the later weeks of larval life, when the maggots have attained a considerable size, and also provides for the maggot when it is ripe a way out of the host's body ; it works through the skin, falls to the ground, seeks shelter, and pupates (Plates II, III, XVI).

Many more examples might be given, but these are sufficient to indicate how often an insect's behaviour at some period of its life has reference, not only to its present need for food and possibly for shelter, but also to future contingencies in its growth and development which it cannot possibly foresee. These actions are remarkably purpose-like, but the creature that performs them can have no knowledge of their purpose. The tendency to react in certain ways to the environment and its stimulation is part of the insect's inherited nature ; it is so bound up with the story of the race, that many thinkers on these questions who realise that the memory or foresight of the individual can play no part in the appointed process, do not hesitate to idealise that process by suggesting that it implies a "racial memory" so impressed on the species that the appropriate lines of behaviour are followed by adult and larva as one generation follows another.

The behaviour of social insects is a subject of special interest, and some details of this will be discussed in a later chapter. In closing this general sketch of insectan behaviour it may be noted how in many cases a large insect population of the same or of allied species, not practising social life



# PLATE III



A. SKIN OF COW'S THIGH (HAIR CLIPPED) WITH ENTRANCE HOLES OF FIRST-STAGE LARVAE OF *Hypoderma lineatum*.



*a*

B. SECOND-STAGE LARVA OF *H. lineatum* IN SUB-MUCOUS COAT OF GULLET OF BULLOCK. (*a* to *a*, Mucous Coat cut away.)



*a*

C. FINAL STAGE LARVAE OF *H. bovis* IN "WARBLES" BENEATH SKIN OF BULLOCK'S BACK.

To face p. 110.]

[A and B, *H. Britten*, photo.  
[C, *T. Price*, photo.



in the accepted meaning of the term, may undergo marked changes of habit on account of some new factor in their surroundings. Such new factors are often due to man's unconscious intervention, and the resulting changes of behaviour among insects may therefore be noticed by those naturalists who pay especial attention to those insects that feed on plants cultivated as farm or garden crops, or that live as parasites on domestic animals. There is a beetle, a small weevil, *Orchestes fagi*, that is very common on beech trees in this country, the adults eating the leaves into holes, and their grubs mining between the upper and lower leaf-skins. During recent years both in England (F. V. Theobald, 1912) and in Ireland (G. H. Carpenter, 1920) it has been observed that large numbers of these beetles, blown off beech trees into apple orchards, take to feeding on the growing fruitlets—a new kind of tree and a different part of the plant as compared with the normal feeding place of their kind. Also a sucking insect, a plant bug *Plesio-coris rugicollis*, whose normal food is the sap of willow leaves, has been noticed repeatedly since the observations of F. R. Petherbridge and M. A. Husain (1918) piercing the skin of young apples to suck their juice. It is highly probable that these are new modes of behaviour adopted by members of these and other species that have been accidentally brought into touch with a new plant on which they are able to feed.

Similar changes in habit are undoubtedly new departures when they result from a newly introduced factor in the surroundings of the insects that display them. Since the beginning of this century tobacco has been grown in Ireland on a small scale, and a crop in Co. Kilkenny was found to be severely injured by multitudes of springtails feeding on the leaves. These on examination proved to belong to a north European species *Isotoma tenella*, never before recognised in these countries. The minute insects had certainly not been introduced with the tobacco, which was raised from seed, and taking all the facts into consideration, no doubt can remain that the presence of a large number of plants of a



kind new to the country on a comparatively small area, had provided so favourable an environment for the springtails that a species, formerly so scarce as to be overlooked, forced itself on the attention of the cultivators by multiplying so fast as to become a "pest." Here the insects in their thousands all responded in the same way to the stimulation of their new surroundings by feeding on the plants with which they were thus for the first time brought into touch.

Another similar case of a more remarkable kind has been furnished through the introduction of great flocks of sheep into Australia during the last century, and the reaction of this introduction on some Australian flies during the last thirty years. It is well known that in the British Islands and in other countries of Western Europe a greenbottle fly (*Lucilia sericata*), belonging to a group the usual behaviour of whose members is to lay eggs on carrion, has the habit of depositing eggs on the wool of live sheep into whose skin and flesh the maggots when hatched eat their way. (See G. H. Carpenter, 1902, and R. S. Macdougall, 1909.) Such abnormal behaviour is a response which this species has been making for centuries in England to the presence of thousands of sheep in the fields and on the hills; the female fly is attracted by the odorous secretions and excrements of the sheep, and her approach to the animals for the purpose of egg-laying may be regarded as a typical chemotropic action. The student of insect behaviour cannot but wonder why one and only one kind out of the scores of nearly related flies should commonly adopt this habit, at once horrifying and interesting. In Australia, where the sheep-grazing areas have been constantly extended with the advance of human settlement into the interior of the continent, a precisely similar response to the presence of flocks of sheep has been made by at least five or six of the native species of the bluebottle and greenbottle group of flies. W. W. Froggatt (1915-18) has found that besides *Lucilia sericata* and *L. caesar*, presumably introduced from Europe, four Australian species of *Calliphora*, an *Ophyra*, and a *Sarcophaga* act as "Sheep-maggot flies" on the vast

grazings of New South Wales. In connection with the special aspect of insect behaviour now under discussion it is noteworthy that only since 1895, or thereabout, has this habit "become a real menace to sheepowners." Here the introduction into the surroundings of certain Australian insects of large flocks of sheep has led to a response by myriads of female flies which has resulted in their larvae feeding on living instead of dead flesh, and has incidentally affected seriously an important activity of mankind.

These examples of changes in behaviour on a large scale by myriads of individual insects of the same kind serve to emphasise the fact that the habits of these creatures may be remarkably plastic as they are subjected to changes in their environment. While the experimental methods of laboratory study often enable the student to predict with confidence how an insect will react to various kinds of stimulation, the wider survey of insect behaviour as it can be observed by the naturalist in the open country affords evidence that the creature's actions are not universally and unalterably stereotyped. The races of the insect world have reached their present conditions of form and activity through the long and changeable history of many generations, and it is fascinating to be afforded clear glimpses of changes in behaviour which assure us that by careful study of the activities of the living insects around us we can learn at least something of the course of that still unfinished story.

## CHAPTER VI

### REPRODUCTION AND HEREDITY

OUR discussion on Behaviour in the previous chapter has suggested that many of the actions performed by insects depend upon the constitution which they inherit through their parents and ancestors ; the insect comes into the world with its nervous and other systems " set " in special ways, so that its behaviour is as a rule like that of its parents under similar conditions. It is also obvious and generally recognised that insects—like other living creatures—resemble their parents in form and structure even to minute details ; yet beginners in the study of such insects as the moths belonging to certain groups quickly realise that even among a family reared from the same batch of eggs there may be a considerable degree of individual variation. All living creatures arise as the offspring of pre-existing living creatures. It is of interest to recall that less than two centuries ago many learned men believed and taught that such insects as maggots might be " bred " or " spontaneously generated " by dirt or carrion, although these beliefs had long before been confuted by F. Redi (1671), who showed that the maggots which feed in flesh develop into flies, and that no maggots can appear in flesh which is carefully screened so that flies cannot lay eggs on it. The genetic chains of living creatures around us, and including indeed our own race, are so familiar as part of our accepted world that we readily overlook the problems that present themselves when we consider the means by which inherited characters, whether of form, appearance, or behaviour, are passed on through the successive generations



of a race. These problems have claimed much attention from naturalists in recent years, and the partial solution of some of them has been reached through studies on insects by various methods of research, such as the careful microscopic examination of their germ-cells and the tracing out of factors in their inheritance by means of experimental breeding.

Among living beings there are two well-known methods of reproduction, firstly by means of small living units known as germ-cells, secondly by the strong outgrowth of a portion of the organism which may be termed a bud, the bud often separating subsequently from the parent-body. Any kind of reproduction that can be regarded as budding is very rare among insects ; they " increase and multiply " as a rule directly from the germ-cells, to which therefore attention may now be directed.

It has already been mentioned in our Introduction (Chap. I, p. 10) that the germ-cells of insects, as of animals generally, are of two kinds : minute sperm-cells, or spermatozoa, active and mobile ; and comparatively large egg-cells or ova, passive in behaviour and containing more or less food material or yolk (Fig. 3). The sperms are found in the sets of animals that we call males and the eggs in females ; hence the two kinds of germ-cell are sometimes termed respectively male and female cells, but this mode of expression may lead to misunderstanding. It is convenient to have in use a term which can be applied either to a sperm or to an egg, as many features of essential importance in reproduction and inheritance are common to both ; such a term is provided in the word gamete. Many animals—earthworms and snails, for example—have both kinds of gamete developed in the same individual, which is therefore neither exclusively male nor female but hermaphrodite. Among insects, however, hermaphrodites are extremely uncommon.

Reproduction by means of gametes is known as sexual, and for normal sexual reproduction there must be union between the nuclei of gametes of either kind, that is between

an egg-nucleus and a sperm-nucleus. This process is often called the fertilisation of the egg, and fertilisation is usually a necessary preliminary to reproduction. As the egg is relatively large and passive and the sperm is very small and active, the latter moves towards the former ; this it can do because it possesses, besides the ovoid or rod-like head in which the nucleus lies, a long vibratile tail or flagellum by means of which it can swim through fluid. When pairing (copulation) takes place between a male and a female insect a large number of sperms are passed by the former into the reproductive system of the latter. They are stored in a special receptacle (spermatheca) so that they may subsequently fertilise the eggs before these are laid. Among insects, therefore, fertilisation may not occur until some time after pairing. Fertilisation—the union of two gamete-nuclei to form a zygote-nucleus—is the essential starting-point for normal sexual reproduction.

From this brief account it will be realised that the germ-nuclei must play a very important part in the processes of reproduction and inheritance, and these nuclei are bodies of very small size. A male insect's sperm of average dimensions is about  $\frac{1}{30}$  mm. ( $= \frac{1}{700}$  inch) in length, and its head, enclosing the nucleus, may be no more than one-tenth the length of the tail or flagellum. As the head, with the adjacent "centre-piece," is all that usually enters the egg at fertilisation, it is clear that this body must contain all the material necessary for the transmission to an individual of the next generation of the characters, either of structure or habit, that are inherited through the male parent. The formation of the mature flagellate sperms results from a process of development that may often be traced back to an early stage in the life of a male insect. Some essential facts about this development (spermatogenesis) may now be profitably considered as an introduction to our study of inheritance.

Sperm-formation is the result of a special type of cell-division, and it is well known that the development, growth, and maintenance of any living body are due to a series of

cell-divisions in which the cell-nuclei take an important part. The microscopic examination of suitably stained sections reveals in the nucleus of any cell the presence of a substance (chromatin) which takes up the microscopist's stains very readily, and therefore becomes conspicuous. The chromatin often appears in the form of knotted or looped threads, but when a cell is going to divide it becomes segregated in a definite number of minute ovoid or rod-like bodies (chromosomes) each of which splits into two halves—"daughter-chromosomes"—one of these going to form part of the nucleus of either of the "daughter-nuclei" resulting from the cell-division (Fig. 32, *a*). As the growth and repair of all the tissues of the body depend upon an enormous series of such cell-divisions it follows that the number of chromosomes must remain constant throughout the body-cells of any creature, and in a large number of insects (as in other animals) a definite number is characteristic for each kind of creature. A full account of the forms and behaviour of these bodies may be found in the work of L. Doncaster (1920) or E. B. Wilson (1925); only the most essential points can be discussed here, but the student of Insect Biology may profitably remember that a vast amount of information about cell-structure and behaviour which has an important bearing on the life and development of animals generally, has been obtained through the study of insect tissues and germ-cells.

Now, we have seen that in the fertilisation of an egg, the essential process is the conjugation of the two germ-nuclei, egg-nucleus and sperm-nucleus. The number of chromosomes in the zygote-nucleus of the fertilised egg must be clearly the sum of the numbers in the two gamete-nuclei. But if these numbers were the same as in the body-cells of the insect, they would be necessarily doubled after every reproductive pairing, they would be repeatedly doubled throughout successive generations and the creature's nuclear constitution would become impossibly complex. This condition is prevented and the number of chromosomes is kept constant through successive generations by



"reduction divisions" during that maturation of the germ-cells in both sexes which is a prelude to fertilisation.

Sperm-cells are produced by the divisions of cells known as spermatocytes which are the offspring of the primitive germ-cells of the male insect. The primary spermatocytes, like the primitive germ-cells, have the number of chromosomes normal to the male of their kind of insect. But when a primary spermatocyte is preparing to divide into two secondary spermatocytes its chromosomes become associated in couples (synapsis) and the members of a couple, instead of splitting, separate from each other, one passing into either nucleus of the two secondary spermatocytes (Fig. 32, *b*). Thus each daughter-nucleus receives only one chromosome of a pair and the chromosome number is reduced to half that normal for the species. Each secondary spermatocyte divides to form two spermatids, the chromosomes splitting so that their reduced number is maintained, this splitting being indeed in some cases apparent before the completion of the first spermatocyte division. Four spermatids are therefore formed as the offspring of each primary spermatocyte, and up to this stage in sperm-formation all the cells are minute globular bodies. Then each spermatid becomes transformed into an active sperm-cell (spermatozoon) with its compact nuclear head and long vibratile tail or flagellum (Fig. 3, *A*) ready to play its part in fertilising an egg-cell.

The egg has also a maturation process which it must undergo in preparation for fertilisation. Immature eggs (or primary oocytes) are the offspring of primitive germ-cells not differing in aspect from the sperm-forming germ-cells of the male. But the oocyte is much larger than the spermatocyte because within it a quantity of yolk is stored up to serve as food-supply for the growing embryo. As regards the nucleus with its chromatin the maturation-process of the egg is essentially similar to that of the sperm. The nucleus of the primary oocyte undergoes a reducing division (meiosis), by which the nuclear material and the number of chromosomes are reduced to half what they

were in the original nucleus. But as each primary oocyte has only enough cell-substance to make one egg, the two

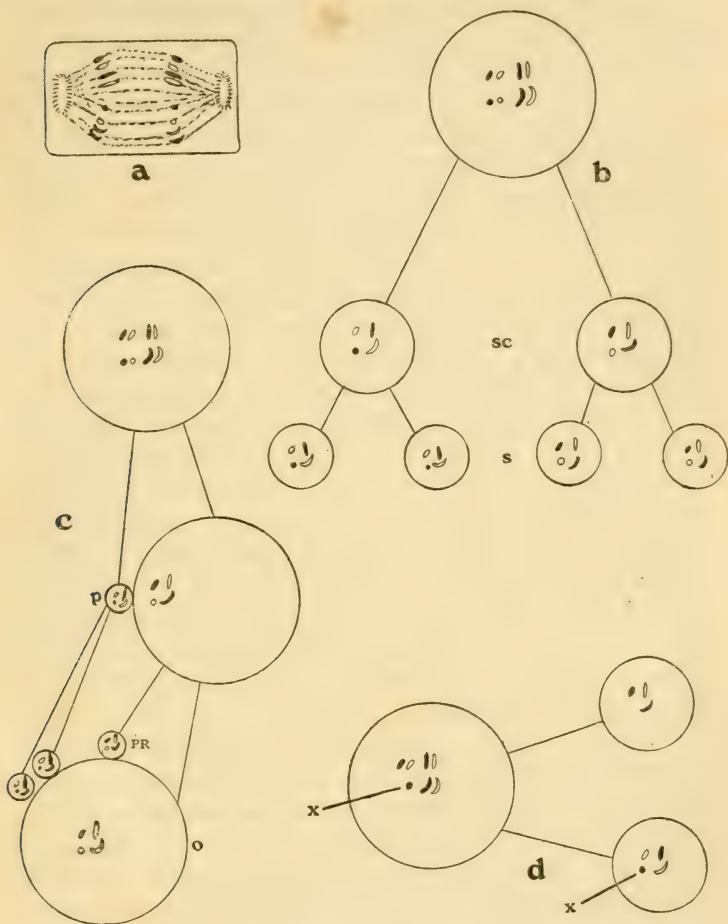


FIG. 32.—Diagrams of (a) normal cell-division (mitosis) with eight chromosomes shown after splitting to form daughter-nuclei; (b) maturation of sperms (spermatogenesis), the primary spermatocyte divides into two secondary spermatocytes (*sc*) with "reduced" nuclei, and each of these divides into two spermatids (*s*); (c) maturation of egg (oogenesis), *p*, 1st polar body and *pr* 2nd polar body. *o*, mature egg ready for fertilisation. *d*, Maturation in a case where the full (diploid) number of chromosomes is uneven, the sex chromosome (*x*) having no partner.

secondary oocytes are extremely unequal in size, one of them, the maturing egg, keeping nearly all the cell-protoplasm and yolk, while the other is a minute "polar body" (Fig. 32, *c*). This division is followed by a second in which (as in the formation of spermatids) each chromosome is split. The egg, now mature, again keeps nearly all the cell-substance, though its nucleus corresponds to that of a spermatid or spermatozoon, while its sister-nucleus, surrounded by a small mass of protoplasm, forms a "second polar body." If, as sometimes happens, the first polar body divides into two daughter-cells it is clear that there are four reduced nuclei (corresponding to the four mature sperm-nuclei), but only one of them becomes the nucleus of a mature egg; the other three have cell-bodies so minute that they can perform no reproductive function, and they were formerly regarded merely as "extrusions" from the ripening egg. The nucleus of the mature egg has however been reduced, so that when the sperm-nucleus enters at fertilisation, the conjoint or zygote-nucleus becomes quantitatively double that of either gamete and the number of chromosomes is restored to that normal for the body-cells of the creature to be developed from the zygote (Fig. 32). In very many insect eggs the polar-nuclei remain within the egg-substance, or the polar bodies after extrusion are reabsorbed by it.

These processes connected with maturation and fertilisation, the more essential features of which have been briefly sketched, have become known through investigations carried out during the last half-century. They were first elucidated by E. van Beneden (1883), T. Boveri (1899), and many students of various animals other than insects; full details of these and subsequent discoveries may be found in the recent text-book of E. B. Wilson (1925). It is evident from the appearance of a definite number of chromosomes in successive generations of creatures of the same kind that there is real individuality and continuity in these bodies and that they are closely connected with the transmission of inherited characters. Half the chromosomes present in the zygote-



nucleus are derived through either parent, and from these are derived by repeated fission all the chromatin in the cells of the body whose development starts from the fertilised egg. Clearly therefore the chromosomes are to be regarded as furnishing the " mechanism of heredity " ; it is somehow through them that " like begets like."

But at the beginning of this chapter we reminded ourselves that offspring may not resemble their parents exactly and that members of the same family may differ from each other. The process of reducing division in the maturation of the germ-cells enables us, partially at least, to understand how such differences, collectively known as variation, are frequently an accompaniment of heredity, because the behaviour of those minute chromosomes within the germ-cell nuclei corresponds with facts that can be observed when the characters of members of the families of successive generations are compared. It is well known that this last-named line of inquiry, pursued with regard to hybridised varieties of plants by J. G. Mendel as long ago as 1865 (see W. Bateson, 1909), has been eagerly followed since the beginning of the present century by many students of various groups of animals, among which certain insects have yielded most important results.

A simple introductory example is afforded by the " Orange " Moth (*Angerona prunaria*) a common British insect of the Geometrid family, the male of which has orange and the female yellow wings, with delicate darkish streaks scattered over the surface, a dark line in the middle of the disc of each wing, and a series of dark dots along the hinder edge or termen. There is a form of this moth, known as the variety *sordidata*, in which the scattered dark streaks are reduced or absent but there is on the forewing a great extension of the dark scaling so as to form two conspicuous bands, one along the termen and the other across the wing base (Plate IV, A). It has been shown by L. Doncaster and G. H. Raynor (1906) that if a pair of these moths, one of the pale type and the other of the variety, be bred together, the offspring will show the

dark banding of *sordiana* together with the streaky scaling of *prunaria* ; these offspring are hybrids, and their hybrid character is recognisable in their appearance although on the whole they resemble *sordiana* rather than *prunaria*. If now such hybrids breed among themselves in numbers, a count of the families of the next generation will show approximately a quarter of the population typical, speckled, unbanded *prunaria*, a quarter unspeckled, markedly banded *sordiana*, while half will be speckled and banded like their parents of the first hybrid family. There is no doubt that these colour patterns depend on inherited characters, and we have seen that there is much reason for believing that the chromosomes in the germ-cell nuclei are concerned with the inheritance of such characters ; as it is now usually expressed, the germ-cells carry the " factors " or " determinants " for them. Recalling the behaviour of the germ-cells in maturation, we remember that at the reducing division the chromosomes are first paired together (one of each pair being derived from either parent), and then separated so that they pass into different mature nuclei. Now it is conceivable that the two chromosome partners in the pairing (synapsis) may be alike, or they may differ in certain factors which they contain ; just so will the mature germ-cells resulting from the reducing division be alike or different as regards those factors. The results of such breeding experiments as those with the Orange Moth agree exactly with the indications afforded by the maturation processes. Call the germinal factor that induces the banding of the wings (in *sordiana*) *S* and the factor for the unbanded wings (typical *prunaria*) *s*. In a strain of pure bred *sordiana* all the germ-cells carry the factor *S*, and in pure bred *prunaria* all carry *s* ; in each case all the germ-cells are alike as regards one of these alternative characters and the individuals of such strains are " gametically pure " or *homozygous*.

When, however, an egg of *sordiana* carrying the factor *S*, is fertilised by a sperm of *prunaria* carrying *s*, the zygote nucleus must contain both factors, and it is from such a

# PLATE IV



A. MALES OF (a) *Angerona prunaria*, (b) its variety *sordiana*, and (c) *prunaria-sordiana* HYBRID.

[After Doncaster & Raynor, P.Z.S. 1904]



B. MALE and FEMALE of *Amphidasys betularia* (left) and of its variety *doubledayaria* (right). Two-thirds size.

To face p. 122.]

[H. Britten, photo.]





zygote that the hybrids produced in the cross-breeding just described are developed. Being hybrids they are *heterozygotes*, their composition as regards the characters under discussion being represented by *Ss*, pure *prunaria* being *ss*, and pure *sordiana* *SS*. In these pure strains all the mature germ-cells produced in any individual carry the factor for one character or the other. But in the reducing divisions which result in the maturation of the hybrid's germ-cells, the pairing of the chromosomes brings *S* always alongside *s*; then they part and go into different gametic nuclei (see Fig. 32, *b*, *c*). So the hybrid produces two kinds of germ-cells each of which must carry either *S* or *s* but cannot carry both. Therefore the pairing of such hybrids may be represented graphically by



and if each individual produces the two kinds of gametes in equal numbers any gamete will have two chances of meeting in fertilisation a gamete of the opposite kind to a single chance of meeting one of its own. Hence, in families of the second generation resulting from the pairings of hybrids among themselves, half the population may be expected to be hybrid, a quarter to be of one pure strain, and a quarter of the other. And this is as a rule closely approximate to the actual result of breeding experiments.

The same principles of inheritance are illustrated, though with an interesting difference in detail, in another common British geometrid, the "Pepper and Salt" Moth (*Amphidasya betularia*). This insect (Plate IV, B) derives its common name from the pale grey colour of its wings, traversed by interrupted black bands which vary considerably in extent and degree in different individuals. The species has, however, a well-marked variety (*doubledayaria*) in which the black scaling is so heavy that the wings present a continuously sooty aspect. It is found that when typical *betularia* is mated with *doubledayaria* all the hybrid

offspring are of the latter variety ; they are indistinguishable from their dark-winged parent and display no evidence of their hybrid nature. The dark wing-colour is " dominant " to the pale ; but when hybrids breed among themselves, the resulting families, if sufficiently numerous in individuals, have three-quarters of their members sooty and a quarter pale. The pale character, hidden in the first generation and reappearing in the second, is known as " recessive." The dark-winged moths of the second generation look all alike, as all resemble their dominant parent, but if the nature of their germ-cells be tested by a study of their offspring, it will be found that a third of them—that is, a quarter of the whole second generation—are pure (homozygous) as to the dominant character, and their inbred descendants will continue to be pure *doubledayaria*, while the other two-thirds—that is, half of the whole second generation—are hybrids (heterozygous) and will therefore give, if bred among themselves, the same proportion of a quarter pure dominants, half hybrid dominants, and a quarter pure recessives as before. The characters of the alternative forms, *doubledayaria* and *betularia* may be indicated respectively by  $D$  and  $d$ . Then the zygote composition of a pure strain of the former will be  $DD$ , and all the gametes must carry the  $D$  factor, while in a pure *betularia* strain the zygote composition will be  $dd$  and the gametes will all carry  $d$ . The hybrids of the first generation must all have the zygotic composition  $Dd$ , and half of their gametes will carry either  $D$  or  $d$ , just as in the hybrid *sordidata-prunaria* the zygotic composition is  $Ss$  and any individual gamete must carry either  $S$  or  $s$ .

In breeding experiments of this kind it is often the practice to make what is called a " back-cross," that is, to mate a hybrid with one of its parent forms. If hybrid *doubledayaria* be paired with *betularia* it is found that in a large enough population half the offspring resemble either parent, as a consideration of their germinal constitution would lead one to expect. For since the hybrid has the composition  $Dd$ , and the *betularia*-parent is  $dd$ , it is clear



that an approximately equal number of *Dd* and *dd* conjugations may be expected.

It was this phenomenon of the dominance of one of a pair of alternative characters over the other (recessive) in inheritance that led Mendel in his classical experiments sixty-two years ago with garden peas, so to analyse the facts of inheritance as to conclude that individual mature germ-cells might carry the factor for one or the other alternative character, but not the factors for both. The processes of maturation, not observed by microscopists until long afterwards, supply the mechanism by which these results are brought about. One most important conclusion that may be drawn from the family histories of these moths is, that while the nature of the offspring may not always agree with the nature of their parents (as in the family of a pair of hybrid *doubledayaria*), it does depend on the nature of the mature germ-cells (gametes) which those parents carry. This is one of many indications of the importance in inheritance of the material which A. Weismann (1893, 1904) called "germ-plasm," a material which we have every reason to believe resides in the nuclear chromatin. It seems at least clear that the factors carried by the chromosomes of the germ-cells determine certain characters of the body. Many other examples, furnished by insects, of the inheritance of alternative characters and of variation might be given, and further reference to these important subjects will be made in later chapters. There is, however, one question which may be considered most suitably here, as it concerns very closely the whole subject of reproduction; that question is the nature and determination of sex. Great uncertainty still surrounds many aspects of the problem, but some remarkable advances towards partial solution have been made during recent years, and much of our knowledge of sex-determination has been reached through investigations on insects.

In many insects as in other animals of which statistical studies on the question have been made, the numbers of males and females in a large population are approximately

equal. It is also evident that in any kind of animal whose members are of one sex or the other, maleness and femaleness may be regarded as alternative characters which might be compared with such characters as dark or pale wings. And it has just been indicated how, in a number of unions between hybrid dominants and pure recessives, we may expect approximately half the offspring to resemble either kind of parent. Further, sex is, in most cases, a truly inborn character. It seems likely, therefore, that the determination of sex follows from what are called "Mendelian" factors; if this be so one sex-factor must be dominant over the other, and members of the one must be hybrid (heterozygous), those of the other pure (homozygous) for the sex-factors. For example, if all males have the zygotic composition  $Mf$ , there will be two kinds of sperms with factors for one sex or the other, while all females will have the composition  $ff$  and all the eggs will be alike carriers of the feminine factor. Such an egg if fertilised by a male-determining sperm will develop into a male, but if by a sperm of the other kind, into a female.

Clear evidence that sex is indeed thus determined in various insects has been afforded by studies of the germ-cells and by breeding experiments. From what has been already stated about reducing-divisions (pp. 117-118) it will have been realised that the number of chromosomes in a zygote-nucleus and in the nuclei of body-cells is commonly an even number—half thereof derived from the gamete contributed by either parent. Many years ago, however, H. Henking (1891) observed that in a bug (*Pyrrhocoris*) two kinds of sperms are produced, distinguished by one kind having a chromosome fewer than the other. Subsequent work by E. B. Wilson and his colleagues (see his text-book, 1925) showed that such a condition occurs in many bugs (Hemiptera) and other insects, whose body-cells have one chromosome less in males than in females, a difference of three or four in the chromosome number of the two sexes (*e.g.* 26 male to 30 female) being sometimes noted. Usually, however, in the body-cells of such differentiated insects the

female is characterised by an even number of chromosomes ( $n$ ) and the male by an odd number, one less ( $n-1$ ). All the mature eggs have  $\frac{n}{2}$  chromosomes, while the ripe sperms have either  $\frac{n}{2}$  or  $\frac{n}{2}-1$ , the latter being clearly male, and the former female-determining. At the pairing of chromosomes for the maturation-process in males of such insects



FIG. 33.—Diagram of Chromosomes of Bug (*Lygaeus*). *a*, Diploid group of male insect in pairs, one "sex-chromosome" ( $x$ ) being much larger than the other ( $y$ ). *d*, Diploid group of female, no such difference apparent. *c*, Maturation division in sperm formation  $x$  and  $y$  separating to the two daughter-groups shown in polar view at *d*, "male-producing" sperm with  $y$ , "female-producing" with  $x$ . After E. B. Wilson (*Journ. Exper. Zool.* ii, 1905).

there is a sex-chromosome which has no partner; therefore in the reducing division half the sperms will receive a chromosome more than the other half (Fig. 32, *d*). In such cases where the male-determining sperm is distinguished by the absence of a sex-chromosome, it seems inappropriate to state that the male-factor is "dominant," though the result is comparable to dominance in ordinary Mendelian inheritance.

It is also of great interest to know that in other insects



the two kinds of sperms are distinguished not by the total absence of a certain chromosome, but by a marked difference in size or shape between the two of a pair. Thus, in a bug (*Lygaeus*) investigated by Wilson, the full (zygote) number is fourteen; in a female the two "sex-chromosomes" are equal in size, while in a male (Fig. 33) one of them ( $x$  the "female-producing") is much larger than the other ( $y$ ). The two members of this unequal pair go into different daughter-cells at any reducing division, and fertilisation by an  $x$ -bearing sperm will result in a female-producing zygote, or by a  $y$ -bearing sperm in a male-producing one.

These facts establish the conclusion that sex-determination is closely dependent on certain factors situated in certain definite chromosomes of the germ-cells. That the same is true for other inherited characters is shown by what is called "sex-linked" inheritance—a term applied to cases in which some readily observed feature in body-structure or appearance is inherited by means of a factor carried in the same chromosome that bears the factor for sex (either male or female). The insects in which this condition has been most thoroughly studied are small Fruit-flies (*Drosophila*) which breed very quickly and prolifically under observation in the laboratory, and are thus particularly suitable for studies in heredity, as a number of generations can be observed in a comparatively short time. Investigations on these flies have been carried on through several years by T. H. Morgan and his colleagues (1916, etc.); only a brief summary of some of the results can be given here. The normal colour of the eyes of some of these flies is red, but a male variety appeared in which the eyes were white. Breeding experiments show that the normal red eye-colour is dominant to white, and that males are hybrid and females pure as regards the sex-factors. The crucial test of sex-linkage is furnished by pairing white-eyed females with hybrid red-eyed males; the offspring of such a cross are half white-eyed males and half red-eyed females. If we indicate graphically the constitution of the parents.

*Male* Rw

♀♂

*Female* ww

♀♀

the two kinds of offspring will be represented by

*Males* ww

♀♂

*Females* Rw

♀♀

and consideration of possibilities convinces us that the sex and eye-colour of the progeny depends on the linkage of the factor for red eyes with that for femininity in half the ripe sperms of the hybrid males. This can only mean that those two factors reside in the same chromosome, which at a reducing division passes into one or other of a pair of sperm-nuclei.

Study of chromosome behaviour in the cells of *Drosophila* is comparatively simple because there are only four pairs of those bodies—one pair minute and round, two pairs bow-shaped and clubbed at their extremities, and a pair of which in the female both members are straight and rod-like, while in the male one is straight and the other sharply bent towards one end. The members of this last pair are the sex-chromosomes, the bent member of the male pair being visibly the *y* chromosome; this carries the factors which determine the male sex and also that which brings about absence of pigment in the eyes. The factor for redness of eyes, if borne in a male *Drosophila*, is linked with that for femaleness in the *x* chromosome. More than a hundred such sex-linked characters have been studied by Morgan and his colleagues in their breeding experiments with *Drosophila*, and the way in which these are grouped in inheritance correspond with the number of chromosomes, four pairs, present in the zygote nuclei.

Mention must be made of a few exceptional results shown by these experiments which, when analysed, are found to throw further light on the part played by the chromosomes in heredity. In the families resulting from the union of hybrid red-eyed male *Drosophila* with pure white-eyed females, the offspring are not always all white-

eyed males and red-eyed females ; sometimes this " criss-cross " inheritance fails to work in some 5 per cent. of the population which appear just like their parents—red-eyed males and white-eyed females. C. B. Bridges (1916), by careful breeding observations confirmed by microscopical study of the cell-nuclei, has demonstrated that these exceptions arise from " non-disjunction " of the sex-chromosomes in the maturation divisions of the egg-nuclei ; the members of a pair of white-bearing, female-determining ( $x$ ) chromosomes may not part company with each other but may both pass into the same daughter-nucleus, so that a ripe egg, instead of carrying the normal one  $x$  chromosome may carry two or none. Bridges has proved that if the former kind of egg be fertilised by a sperm with the male factor the offspring will be the exceptional white-eyed female, while if the egg without any sex-chromosome be fertilised by a sperm with the female and red-eye factors the offspring will be the exceptional red-eyed male. These conclusions are startling when compared with the conditions that apparently determine sex in the normal results of cross-breeding already considered (pp. 128-9). In these exceptional families the white-eyed flies are females although there is a male-factor (which is commonly regarded as " dominant ") in the zygote nucleus. But then there are two female factors, so that we might conclude that the quantity of the respective determinant in the nucleus helps to decide the resulting sex ; the single male-factor may be dominant over one female factor but has to give way to a " double dose " of femininity ! The constitution of the exceptional red-eyed male, however, is still more surprising, for this insect has no chromosome with the male factor ; his only sex-chromosome is female-producing. In view of these facts several students of these subjects, including R. Goldschmidt in his recent (1923) critical discussion of the question of sex-determination, believe that the normal heterozygotic male creature ( $fM$  or  $xy$ ) is a male, not because he possesses the " male " factor ( $y$ ), but because he has only one chromosome with the " female " factor ( $x$ ).



When two  $x$  chromosomes are present the creature must be female.

Sex-chromosomes of the same essential type as those of *Drosophila* have now been demonstrated in other insects of the same order (Diptera) as well as in grasshoppers (Orthoptera) and beetles (Coleoptera). In several types of moths (Lepidoptera), the males are pure and the females hybrid for sex-characters: this was worked out by L. Doncaster (1908, 1914) in his famous studies on the breeding of the Magpie Moth (*Abraxas grossulariata*) with its pale variety *lacticolor*, known only from female specimens, and affording an example of sex-linked inheritance contrasting with that of *Drosophila*. In bees, wasps, and most Hymenoptera that have been studied there is a remarkable difference between the two sexes in the chromosome-number, females having twice as many as males; the meaning and results of this condition will be discussed later in this chapter.

The facts set forth in the preceding pages might be thought to suggest strongly that an insect's sex is a definite and irrevocable character determined by the constitution of the germ-cells of the creature's parents. Yet, there are other facts well known to students of insects which warn us that by resting in such a conclusion we miss part of the truth of the matter. Insects are hardly every truly hermaphrodite, but abnormal individual specimens in which the characters of the two sexes are more or less combined are well known; such creatures are called gynandromorphs. In certain moths in which the male differs from the female in wing colour or pattern and has more elaborately developed feelers than she, such gynandromorphs can be very easily recognised. In the simplest case a moth may, for example, be male on the left and female on the right side, like the "Emperor" Moth (*Saturnia pavonia*) depicted on Plate V, the difference affecting not only the visible ("secondary") characters of wings and feelers, but frequently also the essential organs of reproduction, so that there is on the

left of the body a testis with sperms and on the right an ovary with eggs. In such a case it is likely that in the first division of the egg nucleus one of the daughter  $x$ -chromosomes failed to pass into the cell whence the left side of the body developed, therefore the left side is "male" and the right "female." An alternative explanation is due to L. Doncaster (1914), who noticed that some eggs of moths are binucleate and that both nuclei may be fertilised; if one were male and the other female in composition, each might give rise to the half of a gynandromorph.

K. Toyama (1906) described gynandromorph moths of the common silkworm (*Bombyx mori*), hybrids from a cross of two races, and the caterpillars whence they developed showed a bilateral distinction in the colours (white and dark-spotted) of the larvae of the parents. Instead of the axial division of an insect into right and left halves showing respectively the characters of either sex, gynandromorphs sometimes occur in which the two sets of characters form an apparently irregular "mosaic" pattern. This condition might be explained also by the irregular division, though at a later stage, of the sex-chromosome in those cells where the abnormal tissues and organs arose in development. In the course of the breeding experiments with *Drosophila* many cases of gynandromorphism were observed, and described by Morgan and Bridges (1919). These abnormal insects were often the offspring of cross-breeding and consequently showed divergent body-characters (length of wing, eye-colour, etc.) as well as some of the external ("secondary") features characterising the two sexes. Many of these *Drosophila* gynandromorphs were bilaterally male and female, while others displayed a more or less irregular "mosaic," the eye, for example, on one side being divided between the alternative colours that are sex-linked in inheritance. Analysis of the results together with knowledge of the nuclear constitution of the various forms, enabled the investigators to demonstrate that all the characters displayed in such abnormal insects are sex-

PLATE V



A. EMPEROR MOTH (*Saturnia favonia*) Gynandromorph.

[J. Armitage, photo.]



B. POPLAR HAWK MOTH (*Smerinthus populi*), Female and Eggs. Half size.

[To face p. 132.]

[H. Britten, photo.]





linked, and are due to the absence of one  $x$ -chromosome in the cells producing those parts of the body which show male features. It follows from this that the gynandromorph must be considered as originally a female with the two  $x$ -chromosomes; if in the repeated cell-divisions leading to development one of these be accidentally "dropped out," male features will appear. It is noteworthy, however, that in a bilateral gynandromorphic *Drosophila* only the outward male characters are present. Internally there are right and left ovaries. Where the distribution of the two sex-characters in a gynandromorph *Drosophila* is mosaic and irregular, the female areas always predominate; this confirms the conclusion that the cell division or divisions in which one of the  $x$ -chromosomes "dropped out" came later in development than the primary division of the egg, and it also confirms the originally female nature of the gynandromorph.

Various abnormal hybrid moths afford examples of a mixture of male and female characters which differ in more important respects from the cases hitherto mentioned, as the most remarkable forms show a tendency to transformation from one sex to the other; it is therefore convenient to distinguish them from gynandromorphs, and they have become generally known in recent years as "intersexes." The best known work on such insects is that of R. Goldschmidt (1916-17, 1923), who has made extensive breeding experiments with various races of the Gipsy Moth (*Porthetria dispar*). As is implied in its specific name, this insect shows very marked sexual differentiation, the female having whitish wings with black cross-markings and feebly pectinate feelers, while the male's feelers are strongly pectinate and his wings show a dark brown ground colour on which the black banding is relatively inconspicuous. The species has a very wide range from Western Europe to Japan (the indigenous British race is extinct), and shows well-marked geographical forms. In Goldschmidt's experiments, various Japanese varieties were cross-bred with the European forms of the

moth or with one another. In the earlier experiments European males were crossed with Japanese females and the offspring were all normal as regards sex, but when Japanese males were bred with European females the offspring grew into normal males and into females with a blend of male characters. Later, when a number of distinct races had been tested, it was found that "the extent of intersexuality is definite and typical for a particular cross," so that the intersexes could be sorted into low, middle, and high grades. Extreme members of the last-named group were actually males in appearance and behaviour, and microscopic examination of the reproductive organs showed degenerate eggs, the ovarian tissue becoming displaced by spermathecae, and ripe sperms being produced. It is possible also to produce male intersexes tending to develop feminine characters though less completely than the modified or transformed females just described.

These facts suggest that, at least in insects like the Gipsy Moth which produce intersexes, the sex cannot be absolutely determined by the  $x$  or  $y$  chromosomes. In moths, as we have seen, the male is homozygous ( $xx$ ) for the sex factors. Goldschmidt seeks an explanation for intersexes by assuming the existence of a factor for femininity ( $F$ ) in addition to the normal male sex-factor that resides in the  $x$  chromosomes. The hypothetical female factor, "purely maternal in inheritance," may be supposed to reside in the egg-cytoplasm or in the  $y$  chromosome, and intersexes are believed to be produced when the quantitative strength of the male factors in the fertilised egg is sufficiently high to overpower the tendency to femininity; in extreme cases the potential female is actually transformed into a male. These startling results appear in hybrids because the sex-determining power of one parent-race is higher than that of the other.

At least we must conclude that these results show the possibility of modification of the ordinary type of sex-inheritance. But there is no apparent doubt that such modification in insects is always brought about by means



of some factor in the germ-cells whose influence, once impressed on the cells developing into the body-organs and tissues, cannot be set aside. It has been shown by J. T. Oudemans (1898), J. Meisenheimer (1904), and others, that removal of the ovarian or testicular rudiments from a caterpillar has no effect in preventing the normal development of the outward female or male characters respectively, nor does the transplantation of an ovarian rudiment into a castrated male insect modify at all the normal growth of its visible male characters. The development of secondary sexual characters and their partial transformation by means of internal secretions are well-known facts in the physiology of birds and mammals, but there is no evidence of any such agency in producing the often conspicuous sexual differences among insects; these differences seem always germinal in origin.

It has indeed been seemingly demonstrated through V. G. L. van Sommeren's surprising experiments, recently recorded by E. B. Poulton (1927), that varying degrees of gynandromorphic modification in butterflies can be induced by "mechanical shock," applied during the casting of the last larval outside while the pupa is "still soft and moist." The insects were "shocked" by the experimenter "knocking several times with the knuckles or a mallet of medium weight" on a box from the side or top of which the pupating caterpillars were suspended. The subject of this investigation was the African *Papilio hirsutus*, which displays marked sexual characters, as there are several forms of the female differing from the male in the absence or "size" of the hindwings, as well as in complete divergence of wing-patterns, for these various females resemble closely in aspect females of other families, affording excellent examples of "mimicry" among insects (see Chapter XII, pp. 350-355). Some of the female individuals that emerged in the course of these experiments showed at one side more or less approach to the male in wing-pattern, and some of the males more or less approach to the female aspect, denoting "a state from a minute trace of gynandromorphism up to a

very nearly complete half-and-half example." According to Poulton's interpretation these effects can be produced because the formative pupal tissues retain to some extent the embryonic potentialities: "the pupal factors which determine the secondary characters of sex are in a condition analogous to that of a Mendelian heterozygote . . . and the underlying characters are revealed by a correctly timed mechanical shock." The shock is apparently able to affect even in the developing pupa these factors, which are continuous, we may believe, with the factors of the germ-cells.

That the chromosomes supply the mechanism through which inherited characters are passed on through successive generations seems to be well established by the facts that we have considered; the linkage of various factors in the same chromosome affords strong support for this view. It is interesting to notice that further evidence has been deduced from exceptions to the ordinary linkage phenomena that have been observed by students of heredity in many groups of animals, and notably by Morgan and his colleagues in *Drosophila* (1922). They believe that they have succeeded in locating the factors for a large number of varying characters in one or other of the four chromosomes in the gametes of this fly, and finding that the inheritance of these characters is not always according to expectation—for example  $\frac{AbcD}{aBCd}$  instead of  $\frac{ABCD}{abcd}$ —they conclude that, when the chromosomes are paired for the reducing division and more or less closely twisted or looped in certain regions of their length, there may be a fracture and exchange of parts between the two chromosomes of a pair; the frequency of this occurrence, known as "crossing over," can be observed, and from subsequent calculations the investigators believe that they can "map" the chromosomes so as to determine approximately how the factors of the various characters are arranged along their length.

From the preceding statements and discussion one

important limitation of the evidence must be admitted. All the characters whose inheritance by means of the chromosomes has been clearly demonstrated, are detailed characters—varietal or specific. It is extremely likely that the factors for the more fundamental characters—those, for example, which distinguish a fly from a moth or a bee—are also situated in the chromosomes, but some students of the problems of heredity believe it possible that these may reside rather in the cytoplasm of the germ-cells, especially perhaps in the egg-substance. In connection with this possibility, it is of interest to note that definite bodies granular or rod-like (chromidia) and also reticulate (“Golgi-bodies”), have been now observed in the body-cells and germ-cells of many insects as of other animals. In some cases these bodies appear to undergo a definite and regular process of division when the cells are dividing, so that their individuality and continuity may be inferred. Possibly, as some students of the subject have supposed, they are nuclear in origin, and may be the agents by means of which the nucleus influences the substance of the cell. For information on these bodies reference may be made to the writings of Wilson (1925) and J. B. Gatenby (1917-19).

So far we have considered the working of inheritance and reproduction among insects along the usual lines of the sexual process common to the great groups of animals generally, the new individual developing from the fertilised egg. It is well known, however, that in many animals cases of development from an unfertilised egg occur, sometimes exceptionally, and sometimes as part of the regular life-cycle of the creature. Study of the reproduction of insects shows some of the most remarkable and interesting examples of this virgin-generation (parthenogenesis) that the animal kingdom affords.

Not a few female moths that had never paired with a male have been known on occasion to lay eggs from which caterpillars were hatched to be in due course transformed into moths; the Common Silkworm (*Bombyx mori*) and



the Gipsy Moth (*Porthetria dispar*), already referred to in this chapter, are examples of species as to which perfectly reliable observations have been made. Such exceptional instances of virgin reproduction are of much interest because there can be no doubt that, in the history of animal groups, regularly occurring parthenogenesis is a condition secondarily derived from reproduction through normal sexual union, and that as a starting point for what is now regular parthenogenesis, we must look to an originally exceptional appearance of this mode of development.

There are insect species of various orders in which parthenogenesis is the usual method of reproduction, males being exceedingly rare in some cases and altogether unknown in others. Of greater interest, however, are those specialised insects in which virgin reproduction alternates definitely in the life-cycle with the usual sexual method. The Aphids (plant-lice or "green-fly") afford the best known example of this cyclical or seasonal parthenogenesis. Among most aphids there are males and females which pair in autumn, and the females lay fertilised hard-shelled eggs which carry the race over the winter. From these eggs females only are hatched, "stem-mothers" as they are called, whose eggs without fertilisation develop within the oviducts of the female so that active young are born. Successive generations of such "viviparous" virgin females follow each other through the spring and summer, those of the latest brood giving birth to males as well as to the sexual females of the autumn. Here there are many generations in the course of the yearly life-cycle. The Cynipidae or Gall-flies, a well-known family of the Hymenoptera, have not more than two alternating generations in the year, usually a summer sexual brood, and a winter or spring brood consisting of virgin females only. Among many at least of the social Hymenoptera (ants, wasps, and bees) the mother or "queen" insect may lay either fertilised eggs from which females are normally developed, or unfertilised eggs which as a rule only produce males. In these insects, therefore, the occurrence of parthenogenesis seems

to be strangely connected with the determination of sex. It appears at first sight anomalous that in an ordinary community of hive-bees all the male members ("drones") should be without any inherited characters derived through a male parent, but as the queen-bee develops from a fertilised egg, each drone has a maternal grandfather.

In many of these cases the facts of virgin-reproduction have been proved to correspond with some abnormal mode of nuclear division among the germ-cells. Thus in Aphids and their allies the Phylloxerans, T. H. Morgan has shown (1909) that the eggs of the parthenogenetic females mature without reduction; only one polar body is extruded and the number of chromosomes remains at the full "diploid" complement ( $2n$ ). In the sexual broods of aphids which produce the winter eggs, while the females have the full double number ( $2n$ ) the males have one or two fewer ( $2n-1$  or  $2n-2$ ). This is brought about by a partial reduction during the maturation of the male-producing eggs of the virgin females of the last generation, one or two chromosomes passing undivided into the polar-nucleus, so that the ripe-egg nucleus has one or two fewer than the full double number. It has been mentioned that the fertilised winter eggs, which the sexual aphids produce, all develop into female insects, when hatched the next spring. In the spermatogenesis of the autumn males the usual reduction-division takes place, but only those spermatocytes whose nuclei contain the full single ("haploid") number of chromosomes ( $n$ ) develop so as to give rise to active spermatozoa; all those without the  $x$ -chromosome ( $n-1$  or  $n-2$ ) are much below the normal size and cannot produce functional sperm-cells. Hence it follows that every fertilised egg has the full diploid number of chromosomes and develops into a female insect.

Among the Hymenoptera, as has already been mentioned, the number of chromosomes in the cell-nuclei of a male insect is half the number that characterises the female's nuclei; in bees, for example, a male's nucleus has sixteen

and a female's thirty-two chromosomes. F. Meves (1901) and others have shown that in the female egg maturation pursues its usual course so that the ripe egg has only sixteen. In spermatogenesis, however, the first maturation division is abortive, a small cytoplasmic body being divided off from the spermatocyte which retains all sixteen chromosomes in its nucleus. Then in the succeeding division these are, as usual, split so that each of the two resulting spermatids has sixteen chromosomes. Hence it follows that an unfertilised egg (with sixteen chromosomes) will develop into a male or "drone" bee, while a fertilised egg (with thirty-two chromosomes) will develop into a female bee, either a "queen" or a "worker"; which of these two latter alternative results will be produced depends upon the treatment and feeding of the larva, a striking illustration of the co-operation of the factors of heredity and environment—of "nature" and "nurture"—in bringing about the final result of the reproductive process.

The origin of females from fertilised and of males from virgin eggs has long been recognised as the general rule among the bees, wasps, and their allies. Some careful breeding experiments by W. Newell (1915), who crossed yellow Italian bees with members of a grey race, afford confirmation of the accepted view. When yellow queens were mated with grey drones all the offspring were yellow, the colour factor for this being dominant to that for grey; but when grey females were mated with yellow drones the workers were yellow but the drones were grey; these latter clearly had no inheritance through a male parent. But from the eggs of hybrid yellow females either grey or yellow drones might be produced. Statements have, however, often been made that drone bees may be developed from fertilised eggs by special feeding of the larvae; if such statements really represent the facts, cases of intersexuality (pp. 133-5) might be supposed. R. W. Jack (1916) has brought forward evidence that cannot be lightly set aside for the occasional development of worker bees from the



unfertilised eggs that may be produced in the rudimentary ovaries of workers, and this might be explained by a suppression of the reduction division in maturation. R. Goldschmidt (1923), in a discussion of such alleged exceptional modes of reproductive behaviour, calls attention to the possibility of non-disjunction (p. 130) in maturation as the cause. "If such an abnormality occurs among the Hymenoptera, it would be possible for ripe eggs to be produced containing two  $x$ -chromosomes as well as ripe eggs with none. The first would give females parthenogenetically whilst the latter would, after fertilisation, give males."

Thus far we have considered the germ-cells and the hereditary factors borne, as we believe, in their chromosomes; these must be regarded as the essential elements in reproduction. They require, however, for their action, many accessory structures and processes which, in the pairing and breeding of insects, are often conspicuous, characteristic, and noteworthy. The eggs of a female insect are developed in her ovaries (Fig. 34)—a pair of organs each consisting of a number of tubes to which the contained eggs as they ripen give a "beaded" aspect. Each egg needs to accumulate a store of food-material (yolk) for the nourishment of the embryo which, it may be hoped, will grow from it; this food-stuff is in many insects obtained at the expense of other cells in the ovarian tube, "nurse-cells" as they are called, which lie in groups between successive eggs, or form a single group at the fine terminal end of the tube, the eggs keeping contact with them by means of protoplasmic threads. Where there are no nurse-cells the "follicular cells," which form a sheet or follicle closely enveloping each egg, supply food material, and each follicle secretes on its inner surface the shell of the egg. This is a relatively hard protective envelope of characteristic shape in various families of insects—globular (Plate V, B), cylindrical, elongate, and rounded at either end (Plate VI, A), flat and disc-like—often adorned with sculptured markings which may indicate the

outlines of the cells that formed it, provided with an opening or micropyle through which a sperm can make its way into



FIG. 34.—Female Reproductive Organs of Warble-fly (*Hypoderma bovis*), lateral view, the right ovary (*ov. r.*) displaced ventralwards; *ov. l.*, left ovary; *od.*, paired oviducts, uniting to form median oviduct (*od\'*) which passes into vagina (*va.*); *sp.*, spermathecae whence three ducts pass to vagina; *ag.*, accessory glands; *op.*, ovipositor; *in.*, intestine; *r.*, rectum with its glands (*rg.*).  $\times 8$ . After Carpenter and Hewitt (*Sci. Proc. R. Dublin Soc.* xiv, 1914).

the living egg-substance, and often with a lid through which the young insect can emerge when the time of hatching arrives.

The number of ovarian tubes and the rate at which the eggs ripen varies enormously in different insects. Some female beetles have only two tubes to each ovary ; most moths have four ; other beetles like the chafers have six ; cockroaches eight ; while a queen-bee has about a hundred and fifty and a queen-termite over two thousand tubes on each side of the body. The ovarian tubes of either side open into an oviduct and the two oviducts lead, in most insects, into a median external passage, the vagina, which has a lining of cuticle being formed by an inpushing of the outer skin. The reproductive passages of insects always open towards the hinder end of the body, and the vaginal aperture is usually situated on or immediately in front of the eighth abdominal segment. Just behind it is the opening of the spermatheca or reservoir into which the sperm-cells pass when the female pairs with a male insect. This spermatheca may be a simple ovoid or sub-globular chamber provided with a short duct, or consist of two or three chambers (Fig. 34, *sp*) with relatively long ducts ; the whole apparatus is lined with cuticle. The typical insect ovipositor consists of three pairs of processes, one of which belongs to the eighth and two to the ninth abdominal segment ; these acting as a forceps hold the egg that is being laid (Fig. 35). The processes of the ovipositor may be relatively short, and usually unseen because retracted into a pouch formed by the inpushing of the hinder abdominal region, or they may project conspicuously at the tail-end of the insect as in ichneumon-flies and many grasshoppers (Fig. 36). In most two-winged flies (Diptera), the processes of the ovipositor are very short, but owing to a great development of the intersegmental cuticle in the hinder part of the abdomen, that region can be extended in a " telescopic " manner when eggs are being laid and retracted again when the organ is out of use (Fig. 35). The well-known sting of wasps, bees, and their allies is a highly specialised ovipositor modified into a formidable weapon of defence or attack, but in some cases retaining still its original function as an egg-laying organ.



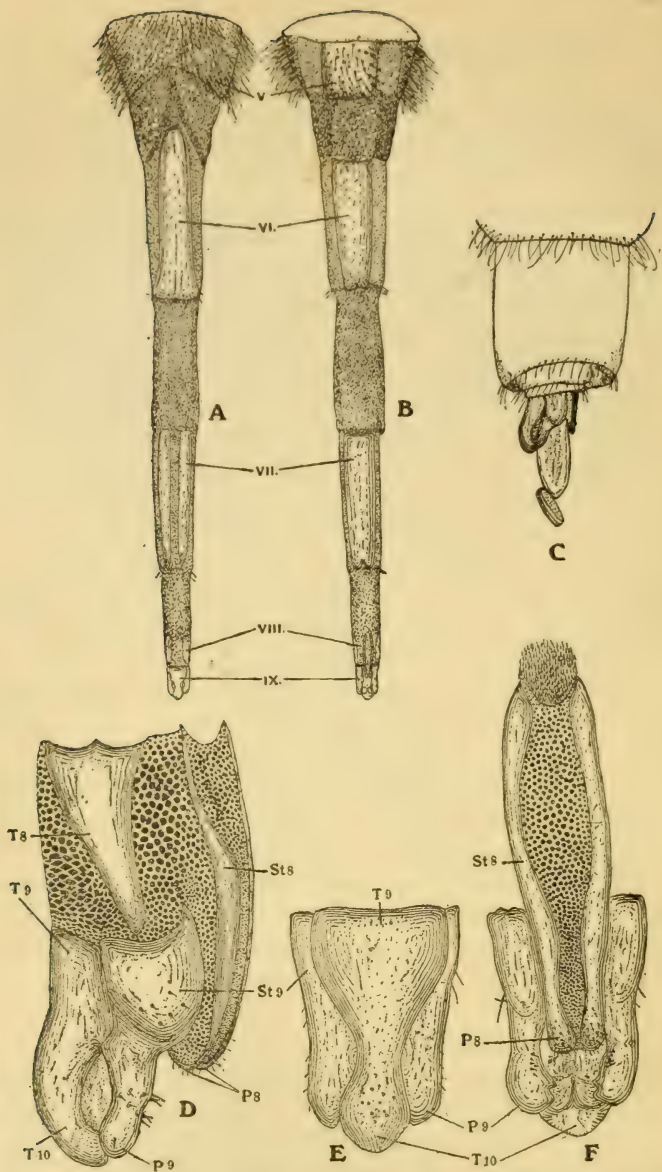


FIG. 35.—A, Dorsal and B, Ventral view of hinder abdominal segments and ovipositor of *Hypoderma bovis*, fully extended; the segments numbered v-i are connected by long intersegmental membranes.  $\times 7$ . C, the same with segments retracted ("telescoped"), the ovipositor holding an egg.  $\times 20$ . D, Lateral, E, dorsal, and F ventral views of terminal segments with ovipositor. The numbers and parts of the eighth, ninth, and tenth abdominal segments are indicated, T, terga; St, sterna, P, processes of ovipositor.  $\times 60$ . After Carpenter and Hewitt.

In every case we find the form and action of an insect's ovipositor suited to the position in which eggs have to be placed. The long ovipositor (Fig. 36, A) of a female phasgonurid grasshopper enable her to bury her eggs deep in the ground, and the long tapering telescopic abdomen of a female crane-fly or carrot-fly enables her to achieve the same result on a smaller scale. The serrated processes of a sawfly's or a cicad's ovipositor serve to cut incisions in plant tissues, while the dart-like egg-laying organ of an ichneumon fly pierces the body-wall of a caterpillar, and prepares for the life of her larva as an internal parasite. Besides laying the eggs the female often fixes or protects them by a hardened fluid secretion of glands opening into the vagina. To such protective action further reference will be made in a later chapter (p. 302).

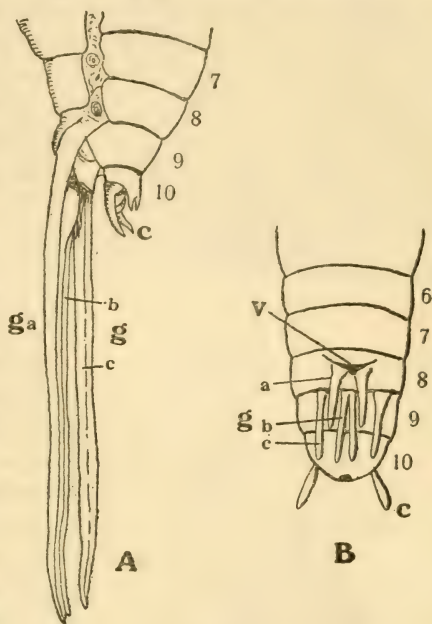


FIG. 36.—A, Hinder Abdominal Segments (7-10) and Ovipositor of Longhorned Grasshopper (*Conocephalus*), lateral view.  $\times 3$ . B, Diagram of Hinder Abdominal Segments (6-10) and developing Ovipositor of a typical female insect. *c*, cerci; *v*, vulva; *ga*, processes (gonapophyses) of eighth segment; *gb*, inner and *gc*, outer processes of ninth segment. After R. E. Snodgrass (*Anatomy of the Honey Bee*, 1909).

The sperm-cells are developed, as already mentioned, in the testes of the male, whose abdomen contains on either side in the dorsal region a testis which corresponds to the female's ovary, and is composed, like that organ, of a number of tubes which open into a duct called, in the male, the

*vas deferens*. The paired vasa deferentia lead into a median chitin-lined ejaculatory duct, which corresponds to the female's vagina, and has associated with it a seminal vesicle, wherein the sperms often complete their development and

await the act of pairing, as well as accessory glands; these secrete a fluid by which, when partially evaporated, the sperms are united in the bundles ready for transference to the sperm reservoir of the female (Fig. 37). In many insects, the drone hive-bee, for example, these accessory glands are of relatively enormous size.

In order to ensure transference of the sperms to the female's spermatheca, male insects are furnished with a cuticular genital armature, corresponding to the female's ovipositor, and used for grasping the female's abdomen in the act of pairing. The ejaculatory duct terminates in an intromittent organ (*aedeagus*) which may be simply tubular as in bristle-tails, or provided with a basal bulb and a set of paired outgrowths as in bees and flies. Pairs of processes on the eighth and ninth abdominal

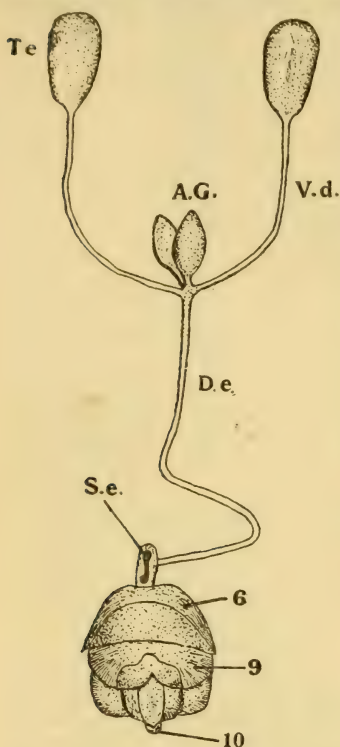


FIG. 37.—Male Reproductive Organs of Warble-fly (*Hypoderma bovis*). *Te*, testis; *V.d.*, vas deferens; *A.G.*, accessory glands; *D.e.*, ejaculatory duct; *S.e.*, ejaculatory sac; 6, 9, 10, terga of the sixth, ninth, and tenth abdominal segments.  $\times 8$ . After Carpenter and Hewitt.

these, serve as claspers working laterally, while the terminal dorsal and ventral plates of the abdomen may be modified into vertically disposed claspers. It is instructive to



compare the simple, primitive armature of a male bristle-tail such as a Machilid with the complex apparatus of a hive-bee, or the still more elaborate structures found in a moth or a muscoid fly (Fig. 38). These outer organs of reproduction, the action of which ensures the fertilisation of the egg, are obviously of great importance to the life of the individual and of the race. It is found that the details of their structure and form are remarkably constant among insects of the same kind differing in definite features from those of nearly allied kinds (in Fig. 38 compare A, B with D, E); the male's structures are thus adapted to fit or interlock with those of his mate so as to transmit the sperms into her reservoir, whence as previously explained, they are discharged as required for fertilisation of the eggs when these are laid.

The foregoing descriptions and discussions suggest that the processes of inheritance and reproduction are closely connected with the vital fact of sex-differentiation, and reference has already been made in this chapter to some of the differences of appearance and behaviour, apart from those directly connected with the reproductive system, that are often conspicuous in male and female insects respectively. Well-known examples of such "secondary sexual characters" are furnished by the brighter, richer, or more vivid colours of many male butterflies, dragon-flies, and other insects as compared with their mates, by the presence of wings in a number of male cockroaches, grasshoppers, moths, and Hymenoptera whose females are wingless, and by the greater relative size and elaboration of sense-organs in the male as compared with the female, as shown in the larger compound eyes of male bees and many flies, the elaborate feathered feelers of many male moths and gnats, the immensely enlarged plate-like feelers, and the strange head and body-outgrowths of many male chafers. Much support is afforded by such facts to the well-known contention of P. Geddes and J. A. Thomson (1889) that male animals express in their organisation the active nature of

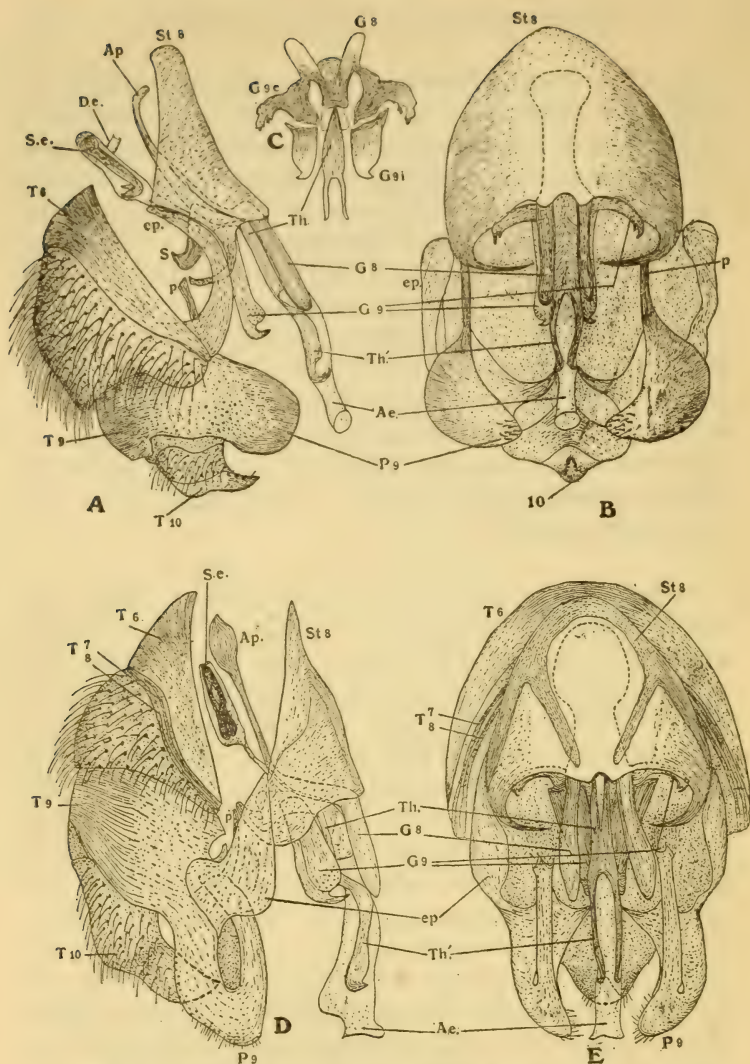


FIG. 38.—Terminal Abdominal Segments and Male Genital Armature of Warble-flies, A, B, C, *Hypoderma bovis*; D, E, *H. lineatum*.  $\times 35$ . Terga (T), Sterna (St.), paired Processes (P), and Gonapophyses (G., G.i., internal, and G.e., external) of the various segments are numbered (6, 7, 8, or 9). D.e., ejaculatory duct.; S.e., ejaculatory sac, with apodeme; Ap., great apodeme; Th., Theca of aedeagus; S., its median spine; Th', its lateral processes; Ae., Aedeagus; p., anterior ridge-process of ninth segment; ep., epipleuron of ninth segment. After Carpenter and Hewitt.

their sex as exhibited in the sperm-cells—an innate tendency towards rapid motion and dissipation of energy, while the larger, quieter, less conspicuous, less aggressive female follows the tendency of the egg to grow excessively and to store up food. It is, however, noteworthy that in the vast majority of insects secondary sexual characters are not conspicuously developed, and the problem remains why these outward differences should be so unequally evident in various members of the same order or family with regard to sex? We have seen reason for concluding that the sex of an individual insect depends normally on the germinal constitution of the egg (fertilised or unfertilised) whence it has developed, while the existence of the gynandromorphs and intersexes warns us that the normal development may, on occasion, be disturbed or side-tracked through some irregular behaviour of the multiplying cells.

Secondary sexual characters and modes of activity lead us naturally to the subject of that behaviour before actual pairing, which is generally known as courtship. It will, however, now be convenient to turn immediately to the manner of growth of an insect from egg to adult, and then to pass on to aspects of courtship in connection with a general discussion on the family life of insects.



## CHAPTER VII

### GROWTH AND TRANSFORMATION

IN the previous chapter we have discussed the behaviour of the germ-cells in maturation and fertilisation, and the power of determination exercised by their germinal constitution on the nature of the insect that may be developed from either the fertilised or the virgin egg. It is well known that between such an egg and the adult of the next generation there intervenes a longer or shorter process of growth and change of form. Some of the more important features of this process must now be described and discussed. In tracing the complete life-history of an insect from egg to adult it is convenient to discriminate first of all between the embryonic development that goes on within the egg-shell up to the appearance of the young insect in the outer world, and the post-embryonic development which occurs after hatching and brings about the growth of the newborn or newly hatched creature into the mature insect capable of reproduction.

As the second of these periods of development is a markedly characteristic feature of insect life, it will be considered in greater detail than the embryonic growth which is common, in some form, to animals generally. Yet the development of an insect embryo presents many features of interest which must not be altogether neglected in our survey of the subject.

Reference has already been made to the relatively large size of an insect's egg, and the amount of food-yolk that is

stored in it. So great is this that the egg-protoplasm necessarily forms centrally a diffuse network, with a condensed circumferential layer within the envelope or shell of the egg; in the central network the yolk spheres, relatively large transparent bodies, are found, as well as a

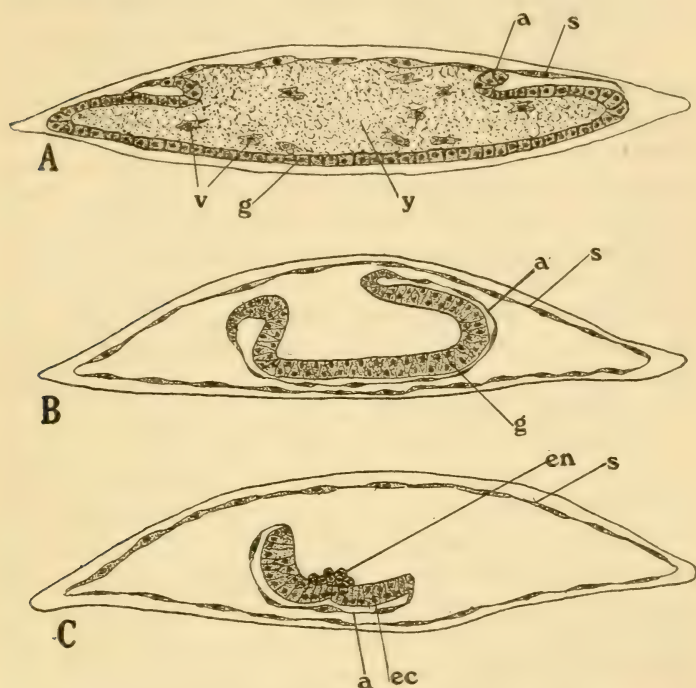


FIG. 39.—A, B, C, Embryonic Development of a Tortricid Moth (*Eudemis naevana*), as shown in transverse sections of the egg-shell with embryo at successive stages.  $\times 50$ . *g*, germ band; *a*, amnion; *s*, serosa; *y*, yolk; *v*, vitellophags (yolk-absorbing cells); *ec*, ectoderm; *en*, inner-cell mass (endoblast or ventral plate). After L. H. Huie (*Proc. R. Soc. Edinb.* xxxviii, 1918).

number of minute corpuscles. The egg thus contains a diffused mass of living protoplasm capable of division and growth, and a quantity of food-material for nourishing the developing embryo. Such a relatively large, heavily yolked egg is common in the great comprehensive group of animals

—the Arthropoda—to which insects belong. The egg shell in most insects is elongate in shape with rounded ends—the eggs (“fly-blow”) of a bluebottle furnish familiar examples, but the most varied forms—spherical, discoidal, cylindrical, flask-shaped—may be seen, and the outer surface of the shell is often marked with ridges and furrows, presenting to the observer a beautifully sculptured aspect.

The embryo (a common term for the unhatched or unborn young) is built up by an orderly process of division (segmentation) of the egg. The zygote-nucleus (p. 117 above) divides in two and the daughter-nuclei divide repeatedly, so that their number rapidly increases. Each nucleus becomes the centre of a protoplasmic mass or cell, though cell-boundaries may not, in the earlier stages of the process, be very evident. As the segmentation of the egg thus proceeds the numerous cells arrange themselves for the most part around the outer region, enclosing a central mass which consists of yolk spheres and corpuscles with a few yolk-cells. Thus there is formed a definite cell-layer or blastoderm surrounding the yolk. Then the blastoderm on one long face of the egg becomes thicker than on the other owing to the deepening of its component cells. The thickened portion or germ-band marks the ventral, the thinner the dorsal aspect of the growing embryo, the inception of which is marked by the insinking of a mass of cells (“middle plate”) along the axis of the germ-band to form a lower layer (endoblast), while the rest of the germ-band overgrows it and becomes the outer embryonic layer (ectoderm); thus the embryo assumes a definitely two-layered condition (Fig. 39). Then by uprising of the thin blastoderm around the germ-band or by the inpushing of the latter into the former a protective layer (amnion) is formed over the embryo (Fig. 39; B, C). Meanwhile the ventral embryonic region becomes definitely segmented owing to the successive appearance of a series of transverse inter-segmental grooves. The early embryo may be regarded as consisting of a primitive head and tail; the remaining segments of the body are formed in succession from before



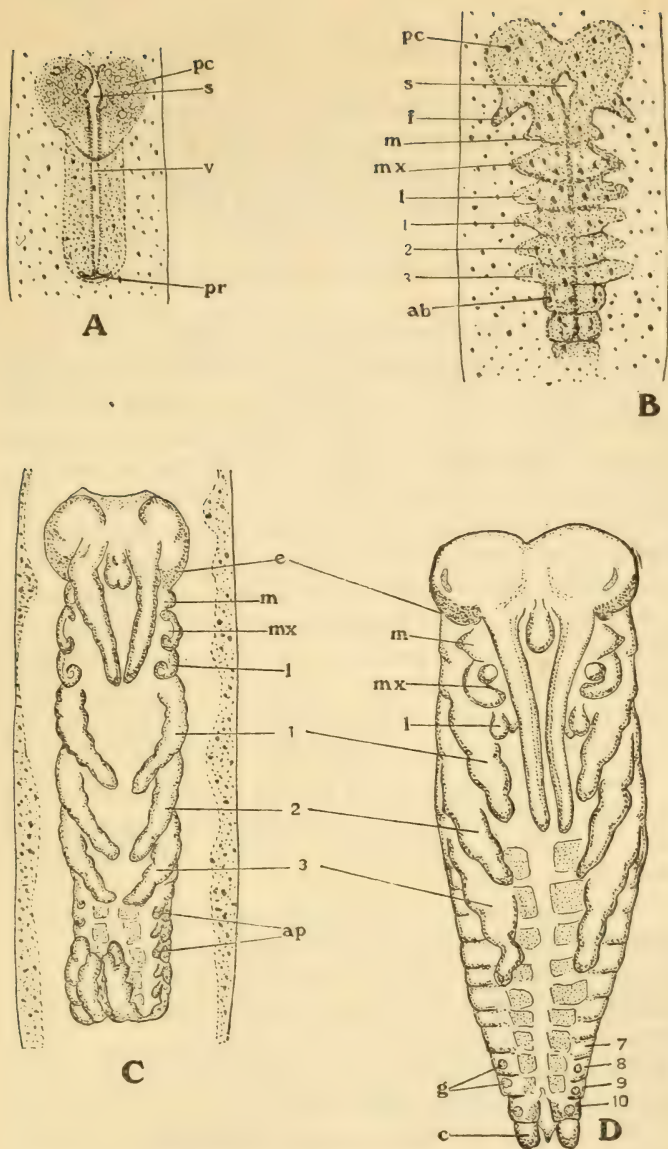


FIG. 40.—A, B, C, D, Stages in Embryonic Development of Grasshopper (*Xiphidium*); surface views of germ-band or embryo from ventral aspect, resting on yolk. *pc*, head lobes; *e*, eye; *s*, mouth (stomodaeum); *v*, ventral groove; *f*, feeler; *m*, mandible; *mx*, maxilla; *l*, labium; 1, 2, 3, legs; *ab*, first abdominal segment; 7, 8, 9, 10, 7th-10th abdominal segments; *ap*, vestigial abdominal appendages; *g*, gonopophyses; *c*, cercopods. Magnified. After W. M. Wheeler (*Journ. Morph.* viii, 1893).

backwards between these two, so that the tail is pushed farther and farther from the head until the whole series of head, thoracic, and abdominal segments have been formed ; and on some of them the rudiments of limbs bud out. This body-segmentation with the series of appendages can be observed on the surface of the developing embryo (Fig. 40).

But deeper investigation by examination of serial sections shows the origin and elaboration of various sets of organs. The outer layer (ectoderm) gives rise not only to the skin (epidermis) but, as in animals generally, to the nervous system, whose rudiments sink in as a pair of elongated segmented ridges whence are formed the series of ganglia with their connecting cords. Fine paired inpushings of ectoderm on most of the segments mark the position of the spiracles and furnish the rudiments of the tracheal or air-tube system. Median inpushings of the ectoderm near the front end of the embryo and at the tail indicate the future mouth and vent, and grow into the fore-gut and hind-gut respectively ; these, it will be remembered (pp. 5, 23-8, 30-1), as well as the air-tubes, are lined with cuticle in the developed insect. As growth proceeds, the mouth, originally in front of or between the feelers, moves backwards so that it comes to lie between and behind the mandibles.

The lower layer is necessarily situated between the ectodermic structures just mentioned and the yolk ; most of it grows to form a series of segmental cell-masses (mesodermal somites) each with a pair of cavities (coelomic spaces). From these cell-masses the muscles and connective tissues of the body are formed, regions of many of them growing out into the developing limbs as they arise. Near the walls of certain of the coelomic spaces the primitive germ-cells appear, and these spaces themselves become the cavities of the reproductive organs and their ducts (ovaries and oviducts in the female, testes and vasa deferentia in the male). The mesoderm grows dorsalwards on either side beneath the ectoderm, forming masses of loose tissue, from this the

heart is formed, and the spaces which arise in the spongy mesoderm (mesenchyme) become extended and coalesce to produce the enlarged blood-containing cavity (haemocoel, see pp. 6, 35) characteristic of insects and of arthropods generally.

There is one important feature of the embryonic growth as to which many insects seem to show a remarkable divergence from animals generally. We have seen that the germ-band early becomes differentiated into outer and inner cell-layers. Of these, the outer (ectoderm) gives rise to the skin and the nervous system as is the case in the vast majority of animals. As a general rule the inner layer of cells (endoderm) becomes the lining of the primitive digestive cavity, and the mesoderm whence the muscular and connective tissues are developed, appears as a derivative of the endoderm close to its junction with the ectoderm. Now in insects, and indeed in most Arthropods, the digestive portion (mid-gut) of the food-canal is much restricted, occupying only a relatively small section of the alimentary tract, the extensive fore-gut and hind-gut being derived from inpushed ectoderm and lined with cuticle. It is certain that in all insect embryos by far the greater part of the inner cell-layer must be regarded as mesoderm, since from it the muscles, and connective and blood tissues are formed, as is typical in animals generally. The feature of insectan embryology still most imperfectly understood is the origin of the mid-gut, and it is not established if any definite rudiment in an insect embryo can be identified as certainly comparable to the endoderm among animals generally. This is a surprising gap in our knowledge of development, since the endoderm is one of the two "primary" germ-layers, usually recognisable as a definite entity in a very early stage of animal growth in the egg.

Three principal alternative interpretations of the origin of the mid-gut in insects have been given by the numerous investigators of the subject. Many early students of insect embryology regarded the yolk-cells as representing the endoderm and giving rise to the mid-gut ; but in more



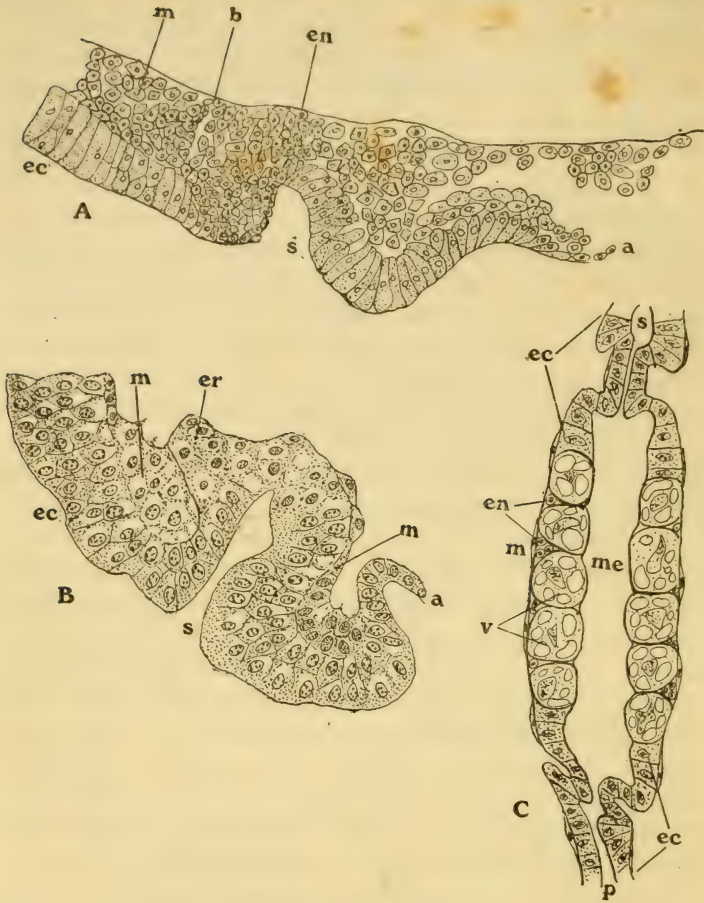


FIG. 41.—Formation of the Mid-gut (mesenteron) in various Insects. A, Longitudinal section through front region of Embryo of Mason Bee (*Chalicodoma*). B, Similar section through same region of Embryo of Leaf-beetle (*Donacia*). C, Longitudinal section through central part of digestive tract of Larval Dragon-fly (*Epithea*). *ec*, ectoderm; *m*, mesoderm; *en*, endoderm; *er* (in B), rudiment of mid-gut (regarded as ectodermal); *b* (in A), boundary of endoderm and mesoderm; *v* (in C), vitellophags (yolk-devouring cells); *s*, stomodaeum (forming mouth and fore-gut); *me*, mid-gut; *p*, proctodaeum (forming hind-gut).  $\times$  about 500. A, after J. Carrière and O. Bürger (*Nova Acta Leopold-Carol. Akad.* lxix, 1897). B, after K. Friederichs (*Ib.* lxxxv, 1906). C, after H. von Tschuproff (*Zool. Anz.* xxvii, 1903).

recent work upon this subject the only reliable support afforded to this view is from R. Heymons' research (1897) into the development of the bristle-tail *Lepisma*, and H. von Tschuproff's account (1903) of the origin of the germ-layers in certain dragon-flies (Fig. 41, C). In the latter case the central portion, in the former the whole of the mid-gut is said to arise from yolk-cells. Most recent workers in this field state that the mid-gut arises from two rudiments which grow from the inner ends of the fore-gut and hind-gut, respectively backwards and forwards, till they meet; the origin of these rudiments appears to prove that they are ectotermal. Such is the interpretation given by R. Heymons (1895) of the development of cockroaches and crickets, by A. Lécaillon (1898) and P. Deegener (1900) of that of various beetles (see Fig. 41, B), and by K. Toyama (1902) of that of the silkworm. But many other investigators of insectan embryology have described the mid-gut rudiments as arising from two cell-masses of the inner layer towards the front and hinder ends of the germ-band, so that they can be fairly regarded as endoderm. Such is the interpretation of W. M. Wheeler (1893) from his studies of the germ-layers in cockroaches and beetles, of K. Heider (1889) in his classical research on the water beetle *Hydrophilus*, of K. Escherich (1900) working at fly embryos, of J. Nusbaum and B. Filinski (1906, 1909) from researches on crickets and cockroaches, of J. Hirschler (1909) from investigations on the development of the beetle *Donacia*, and of J. A. Nelson (1915) in his account of the embryology of the hive-bee, confirming the early account given by B. Grassi (1884) on the development of the same familiar insect and that of J. Carrière and O. Bürger (1897) in their full description of the embryology of the Mason Bee (*Chalicodoma*). These last observers state that the two endodermal rudiments which give rise to the mid-gut in the mason bee embryo appear in those regions of the germ-band where the two ectodermal inpushings produce later the fore-gut and the hind-gut (Fig. 41, A). It may perhaps be possible to find reconciliation between the second and

third views, as set forth here, by supposing that the cell-groups at the inner ends of the two ectodermal inpushings are originally endodermal rudiments which are pushed inwards by the growth of the fore- and hind-gut rudiments of which they appear to form part. It is well known to all students of animal form and development that, largely through the influence of E. Haeckel (1877) and others very great stress has been generally laid on the "germ-layer theory," according to which the two primary germ-layers (ectoderm and endoderm) give rise throughout the animal kingdom to certain definite regions and systems of the embryo. As regards the ectoderm and its derivatives insects appear to follow the general rule, but on any possible interpretation of the facts, there is some abnormality in the origin of the endoderm and its derivatives; this important layer can be recognised only with great difficulty if at all. Heymons, who finds the endoderm in the yolk cells of the embryo of the primitive bristle-tail, believes that in insects generally the original endodermal mid-gut has been replaced by a new one of ectodermal origin. The dragon-fly embryos, in which Tschuproff states that the central region of the mid-gut is derived from yolk-cells and the front and hind regions from ectoderm, might be regarded as indicating a transition between the old and the new conditions.

As the embryo continues to develop, the tissues and organs which in fully formed insects are dorsal in position, tend to grow away from the primitively ventral germ-band, and the yolk becomes surrounded by the cells that form the lining of the gut. The series of appendages: feelers, jaws, legs, assume to some extent their characteristic shapes before the young insect is hatched; at their origin all are much alike, but they become differentiated for various functions as growth proceeds (Fig. 40). It is of much interest to notice that in many insect embryos (that of the grasshopper *Xiphidium*, for example) small paired limbs appear on many of the abdominal segments, but vanish before hatching (Fig. 40, C, *ap*). There may be small or vestigial head-appendages between the feelers and mandibles, and rarely also (J. W.



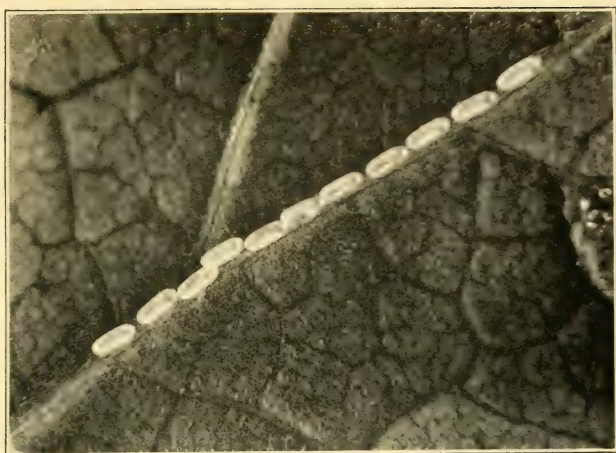
Folsom, 1900) between the mandibles and maxillae. The bearings of such facts on speculations about the racial history of insects will be discussed in later chapters.

The embryonic development of an insect is closed by the experience of hatching (Plate VI, B) which introduces the young creature into the outer world. A necessary preliminary to hatching, as a rule, is the rupture of the egg-case or shell. This may be brought about by inflation of the cuticle of the neck region just behind the head, so as to burst the egg-case, as in the emergence of the young grasshopper, or by the young insect biting a hole through the shell with its mandibles or, as in the case of certain fly-maggots, with its mouth-hooks or with a hard and sharp mouth-spine; or special spinose processes or ridges—"hatching spines"—may be present on the head or prothorax. Such structures, the purpose which they serve, and the manner in which they work are striking instances of what is constantly noticed by students of the life of insects—an apparent prevision of the needs of the creature in succeeding stages of its development, so that it finds itself furnished beforehand with the instruments needed for the next act in its life-drama. The whole course of embryonic development, which has been briefly sketched in the preceding pages, may be regarded as a series of successive events each leading on and preparing for that next to follow, and tending to the construction of the young insect which is to be hatched in due season. Remembering that the process is essentially one brought about by the division and specialisation of cells, we are able to catch some glimpse of the mechanism of the process as we remember that all these cells are derived from the fertilised egg-cell with its complex of inherited factors that render possible the continuity of the racial characters through an innumerable series of generations. The nature of the germ-plasm is such that it can serve as the means for ensuring that the embryo passes through a series of progressive stages that are generally in the same order and of the same nature as those through which its parents and its ancestors passed, each fresh step

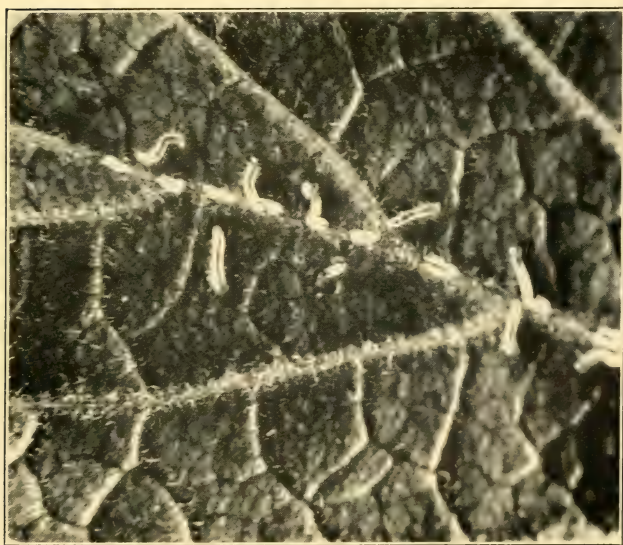
in the process following as a response to some internal or external stimulus. The course of embryonic development, like the programme of instinctive behaviour illustrated in a previous chapter (p. 107), suggests to many students the thought of a "racial memory."

As already mentioned in this chapter (p. 150), the mode of growth of insects after hatching or birth is an especially characteristic feature of their life, and the transformation (metamorphosis) which in many cases is an accompaniment of this post-embryonic growth, has, from early times, arrested the eager attention of observant people. A brief introductory survey of the subject has been given in our first chapter (pp. 10-12); now it requires to be discussed with some fullness and in sufficient detail for appreciation of the essential problems that it presents to the student. It has been noted that an insect's cuticle, being an outer secretion of the skin and not a sheet of living tissue, cannot grow with the creature's growth; therefore it must be periodically shed and renewed. Thus the life-history of an insect is marked by a series of "moult" (ecdyses), which divide the period of its growth into a series of stages. Before the actual moulting process the skin sinks away from the old cuticle, pouring out a "moulting fluid," the secretion in some cases at least, as J. Gonin (1894) and W. L. Tower (1906) have shown, of special large unicellular glands of the skin. Thus there is a fluid-filled space between skin and cuticle. The body now grows quickly, the body-wall, as it is still imprisoned in the cuticle, being of necessity thrown into ridges and furrows to a greater or less degree. Then the skin begins to secrete a new cuticle beneath the old one; this is at first soft and flexible, and necessarily follows the folds and wrinkles of the skin. By the pressure of the accumulated fluid the old cuticle is burst open, generally along a median suture or "line of weakness" in the dorsal region of the thorax; and through the slit thus made the creature in its new cuticle emerges; as a rule the dorsal region of the thorax comes first, then the head with its appendages, then the legs, and lastly the abdomen (Plate I, A),

PLATE VI



A. EGGS OF SAWFLY (*Nematus ribesii*) LAID BENEATH CURRANT LEAF.  
× 4.



B. YOUNG LARVAE OF *N. ribesii* HATCHING. × 3.

To face p. 160.]

[A. G. Britten, photo.]





the old cuticle may slip off backwards and in some cases be turned partly inside out. The cuticular linings of the fore-gut, hind-gut, and air-tubes are shed along with the exoskeleton. After emergence the parts of the creature's body in its new form have room to expand ; the sclerites of the cuticle become firm and darkened so as to assume their characteristic colour, and the successive layers of secondary cuticle begin to form on the surface of the skin beneath the first-formed or primary cuticle. When no longer confined in its " old husk " the insect undergoes a process of expansion through the smoothing out of the folds and wrinkles in the body-wall, so that while it often assumes a form like that which it had borne in the previous stage of its life, it shows soon after the moult a considerable increase in size. Thus through its series of castings and renewals of the cuticle it may grow to a bulk many times greater than it possessed at hatching. Growth accompanied by a number of moults is a necessary feature in the life after hatching of the great majority of insects, and they share this feature with members of other classes of the great group of Arthropoda.

But most insects, when adult, are strikingly distinguished from other arthropods by the possession of wings and the power of flight ; the wings furnish a most distinctive and characteristic feature in the insect's structure. Now, while many insects, such as cockroaches, grasshoppers, and plant-bugs, are hatched in a form generally resembling their parents, displaying the same general build of body, shape, and proportions of legs, nature and function of jaws, there is no trace of wings to be seen on these newly hatched young. Every one knows that such a familiar insect-larva as a butterfly's caterpillar exhibits no trace of wings, and the same condition is noticeable in all insects newly hatched or born. So we see that while insects, like arthropods generally, pass through a series of moults in the course of their growth, the development of the wings that are distinctive of the vast majority of insects is carried on during this post-embryonic period, and that no insect has its wings already formed when it first appears in the outside world.

In the simple direct type of insect-growth, where the young, after hatching, resembles the adult in all essential features, as in grasshoppers, cockroaches, and bugs (Fig. 4), for example, the only marked changes observable in the successive stages are those due to the development of the wings and, in some insects, to the appearance of the female's ovipositor and other processes or appendages connected with reproduction. An insect's wings arise as hollow paired outgrowths of the second and third thoracic segments, their cavities are continuous with the great blood-space of the body and sets of air-tubes grow into them. After the first or second moult in the life-history of a young cockroach or grasshopper the wing-rudiments can be seen as rounded lobes projecting at the hinder corners of the mesonotum and metanotum, and after each successive moult they become larger than before, displaying in some cases, on the surface of the cuticle, branching tracks which indicate the courses of the air-tubes within. The wing-rudiments, which may be regarded as flattened pouches, become more markedly flattened as their areas extend so that they approximate to the condition in the adult insect. But even in the stage before the final moult, the wing rudiments of an immature cockroach, grasshopper, or bug are shorter by far than the wings of the adult insect. It is necessary, therefore, as part of the preparation for this moult, that the wings should grow extensively and rapidly beneath the separated cuticle and thus something of a crisis is apparent at this stage of development. When the last moult has taken place the newly exposed wings are seen to be greatly folded or crumpled, a necessary condition of their extensive growth beneath the cuticle of the penultimate instar. When exposed they unfold and flatten from the base outwards, the cuticle becomes hard and firm, and the floor and roof of the hollow outgrowth of the body from which the wing arises become approximated together except along the courses of the air-tubes where the thickened cuticle forms the supporting tubular nervures or "veins" of the wing.

In such life-histories as those that have been briefly



described, the young insect, all through its growth in general aspect, and indeed in many details of structure, resembles the adult, and its wing-rudiments appear at an early stage as outgrowths of the two thoracic segments that carry the wings. Such insects undergo no marked transformation ; a young grasshopper has the long leaping legs, and a young cockroach the flattened body and rounded



FIG. 42.—Forms of Vine Aphid (*Macrosiphum viticola*), America. A, newborn young,  $\times 70$ ; B, nymph with wing-rudiments,  $\times 20$ ; C, winged virgin female,  $\times 25$ ; D, adult wingless female,  $\times 35$ . After A. C. Baker (*Journ. Agric. Res. U.S.D.A.* xi, 1917).

pronotum of their respective parents. In a study of the biology of insects it is noteworthy that the similarity of form between adult and young goes along with the similarity in the mode of life ; young cockroaches in various stages of growth may be found along with adults sheltering in cracks of walls or lurking beneath hot-water pipes in houses, while young grasshoppers and locusts walk or leap among herbage

and devour leaves as their parents do. A very familiar example of this likeness of the young to the adult in habit and in form is afforded by the Aphids or "greenfly" (Fig. 42). In the spring and summer virgin female broods of these abundant insects, the mother may be seen on a leaf of her food-plant surrounded by her large family of newly or lately born young. They have the same general aspect as their parent, the same tapering abdomen with its prominent, paired cornicles, and they feed in just the same way by piercing the plant-tissues and sucking thence a continual supply of sap. Newly born aphids are, of course, all wingless, and it is interesting to find that in a large proportion of the spring and summer females (Fig. 42, D)—produced in a series of virgin generations—wings are never developed, so that the adults, never wandering far from their birthplace over their native plant, remain wingless like the new-born young. In many of the aphid summer females, however, wings are developed (Fig. 42, B, C) from outward rudiments that increase in size after each moult, and these winged individuals can fly away to other plants so as to extend their feeding-ground. Among the aphids the absence of wings accompanies passivity of habit, and the same connection is still more strikingly shown by whole groups of insects that pass their lives, from egg to adult, on the bodies of animals, deriving thence their food-supply, such as the Anoplura or blood-sucking lice, and the Mallophaga or biting lice which nibble at the hairs or feathers or bite the skin of their mammalian or bird hosts. These groups are entirely wingless throughout life and afford interesting examples of the association of winglessness with the parasitic habit among insects. Here, as might be expected, the adult differs from the newly hatched louse in little except size and the development of the organs of reproduction. As no wings appear, the series of moults through which the insects pass is marked by the smallest possible change of form.

Where, however, the insect in its earlier stages lives among surroundings or under conditions differing from

those of the adult, we find, as a rule, more or less difference in structure, and such difference involves transformation of a greater or less degree in the course of the life-history. For example, there are two families of sucking-insects—the Psyllidae and the Cicadidae—related to the aphids mentioned above. Aphids undergo little or no change of form in the

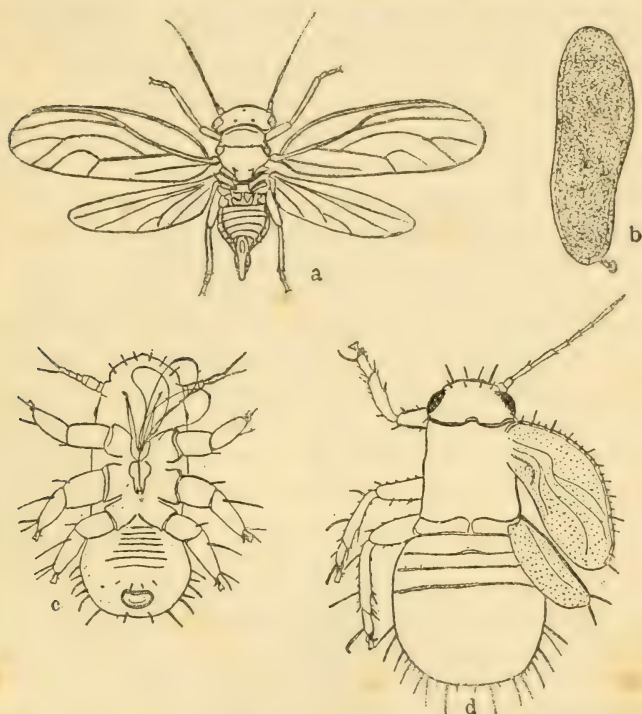


FIG. 43.—Apple Sucker (*Psylla mali*). *a*, female,  $\times 8$ ; *b*, egg,  $\times 80$ ; *c*, first-stage larva (ventral view),  $\times 100$ ; *d*, nymph, fifth instar (dorsal view with legs shown on left, feelers and wing-rudiments on right),  $\times 20$ . After G. H. Carpenter (*Econ. Proc. R. Dublin Soc.* i, 1909).

process of their growth, and young or adult aphids usually live, as we have seen, under much the same conditions. But in the life-cycle of a psyllid or a cicad striking changes of form are to be noted, the young of these insects living in conditions quite different from those of the adult. Psyllids



or "suckers" are active little insects with firm cuticle, a body of considerable depth dorso-ventrally, relatively long feelers and legs, and well-developed wings (Fig. 43, *a*) ; they fly and leap on the shoots of plants whose sap they suck for food. These insects in their young stages are found between the leaves of partially opened buds or clinging to the under surface of the foliage, or in cavities due to the folding or crumpling of leaves apparently resulting from a response evoked by the irritation of the insect's presence, or in definite galls arising in the same manner. In correspondence with such environment, the young sucker has a flattened body relatively broader than that of its parent, rounded in front and behind. The early stages of the Apple Sucker (*Psylla mali*) have been described by Carpenter (1910) and by Awati (1915). In the newly hatched young the feelers and legs are short with fewer segments than in the adult, and the head seems to be fused with the thorax, as there is no division dorsally between crown and pronotum, while ventrally the beak lies between and behind the bases of the fore-legs. The cuticle is relatively soft and thin, and the young insect differs so markedly from its parent that it may be called a larva—the general term (meaning literally a "mask") applied to any young creature which has to undergo transformation before it reaches the adult state. The larval apple sucker (Fig. 43, *c*), after hatching from its curiously stalked egg, wanders to a blossom-bud outside which it waits until the scale-leaves open sufficiently to allow it to crawl inside. Then amid the soft, crowded, developing young leaves it finds shelter and abundance of food, so that it grows quickly, passing through five stages within the bud. In the second of these, as in the first, no wing-rudiments are evident, but in the third and subsequent stages wing-rudiments appear on the thorax ; the creature has now become a nymph whose general body-form is still markedly different from its parent, the prothorax not yet marked off from the head, though the feelers and legs begin to approach the adult proportions. Each of the first three stages lasts about a week, the two later nymph stages

(Fig. 43, *d*), in which the wing-rudiments are well-developed and the cuticle is relatively firm, each last for ten days or a fortnight. After its fifth moult the wings are fully developed and the sucker assumes the adult form.

Cicads are much larger insects than suckers or aphids ;

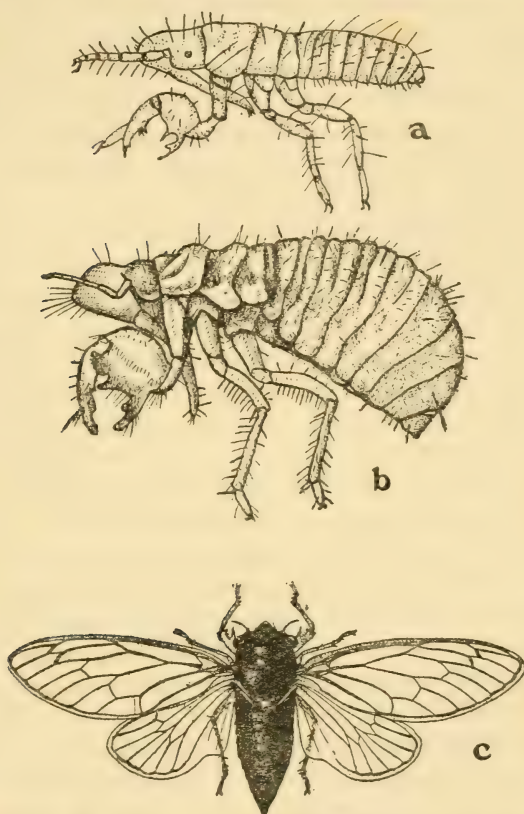


FIG. 44.—Seventeen-year Cicad (*Tibicina septendecim*), North America. *a*, first-stage larva,  $\times 20$  ; *b*, fourth-stage larva,  $\times 5$  ; *c*, female, natural size. After C. L. Marlatt (*Entom. Bull.* 71, *U.S.D.A.* 1907).

they form a prominent feature in the insect fauna of most warm and tropical regions, but they are represented in England by a single species, found only in the south, and there but rarely. They have robust bodies, and broad

heads with large eyes and short feelers ; the front legs are stouter than those of the middle and hind pairs. They have ample wings and fly about in the woodland regions alighting on trees from whose leaves they suck sap. The habits and life-history of the common North American *Tibicina septendecim* (Fig. 44) have been well described by C. L. Marlatt (1907) and R. E. Snodgrass (1921). The female cicad possesses a long cutting ovipositor wherewith she excavates slit-like cavities or " nests " in the twigs of trees and deposits her eggs therein. The young, when hatched, live for a time crawling about the branches of their native tree and then drop to the ground and burrow into the soil. The newly hatched cicad-larva (Fig. 44, *a*) differs from its parent by its soft, pale cuticle, its elongate ovoid head with relatively long feelers and small eyes, its regularly segmented body with little differentiation in the various regions, and its very broad and powerful fore-legs with the spinose tip of the shin adapted for burrowing. The successive stages of the life-history are passed underground, and during these the foot (tarsus) of the fore-limb, well developed in the newly hatched young, becomes greatly reduced. In the two well-marked races of *Tibicina septendecim* it is well known that the growth and transformation of the individual insect is carried on through a period of twelve and sixteen years respectively. Such excessively lengthened life-cycles afford extreme instances of a condition often to be noticed in insect development—a prolonged period of preparation through most of which the creature feeds and grows, leading up to a comparatively brief adult existence the beginning of which usually marks the end of growth and change, and which, whether the creature's way of life and manner of feeding are like or unlike those of its early stages, is strikingly curtailed in its relation to the prolonged period of immaturity.

In their manner of development cicads display yet another feature of much general interest. After the long underground life of years during which the creature feeds by sucking sap from roots which it pierces with its needle-



like jaws, there follows before the emergence of the winged adult, a long period of quiescence. The nymph in its last stage, with its front feet again developed, and displaying prominent wing-rudiments, rests motionless in its earthen burrow for several days or weeks, taking no food while it awaits the time of its final moult. All immature insects suspend their activities for a while when preparing to shed the cuticle, and we have already noticed that the final moult, as it precedes the full development of the wings, marks always something of a crisis in the life-history; the stage leading up to this may therefore be regarded as naturally suitable for prolongation into a definite resting stage. It is noteworthy that such a quiescent interlude is to be seen in the life-histories of insects of several families allied to the cicads and classed in the same sub-order (Homoptera) as they. Thus the Coccidae (mealy bugs and scale insects) and the Aleyrodidae (Plate I, B) pass through a resting stage which may indeed begin at a comparatively early period of the development, before the last moult but one or the last but two; in these insects, however, though motion ceases, feeding by suction may go on. Scale insects and snowflies exhibit a remarkable modification of the moulting process in connection with these resting phases. The old cuticle, after separation from the skin, is not cast off, but becoming hard and firm serves as a protective case for the creature in the comparatively thinly-coated condition that characterises it during the next stage; an emerging snowfly may thus have to make its way to the outer world through three successive discarded cuticles. A striking feature of the life-history of many Coccidae is that the female scale insect never emerges at all; while the male develops wings the female not only remains wingless when adult (like the summer aphids already mentioned in this chapter), but passes the rest of her life and lays her eggs under the sheltering "scale," which consists of the last-shed cuticle strengthened and enlarged by waxy secretions of the skin.

In the insect life-histories so far sketched in this chapter we have seen that the newly hatched young may resemble

generally or differ markedly from its parent, as a rule, according as its mode of life is the same or diverse, and that, in either case, the process of development is largely concerned with the acquisition of wings, while before the final perfecting of these organs there may be a prolonged resting period. We pass on now to consider some life-histories of another type which prevails among the great majority of the insect families. After comparison of the two types it should be possible to appreciate the essential difference between them.

It is a matter of common knowledge that most insects during their life-histories pass through a marked transformation (metamorphosis); the change of a caterpillar into a butterfly, for example, is familiar to every one, and hardly less familiar is the fact that maggots feeding in dead flesh or carrion are the offspring of bluebottles, and that into bluebottles they will in due course be changed. The caterpillar displays many conspicuous features of divergence from its parent butterfly, and the maggot is still more dissimilar to the bluebottle. In the process of transition from the one to the other there must evidently be a considerable amount of reconstruction, and it is therefore not surprising that in the stage preceding the adult, the insect is a quiescent pupa, remaining usually motionless and taking no food. We have already seen that in several groups of insects—cicads, scales, thrips—whose growth exhibits far less marked change of form than the growth of a butterfly or bluebottle, there is partial or complete passivity during the penultimate stage. The quiescence of the pupa, then, is not the essential feature that distinguishes what is generally called “complete” from “incomplete” metamorphosis; it is necessary to seek farther for the true distinction.

The caterpillar hatched from the egg of a butterfly or moth differs conspicuously from its parent, but the differences are in details of structure, not in the fundamental plan of the body. A caterpillar (Fig. 45) has the typical insectan head with all its appendages and organs present, though several of them are simplified or specialised as compared with those of most adult insects; thus the feelers

are very short and inconspicuous, the compound eyes are replaced by a few ocelli, and the maxillae have very short palps and reduced lobes, but the labium though small has its central ligula drawn out into a spinneret whence the silken thread formed as a secretion of the specialised salivary or silk glands, is passed out. The three segments behind the head obviously make up the thorax of a typical insect, as each carries a pair of jointed legs; yet the caterpillar's leg is very short compared with that of the butterfly, its foot-segments are undifferentiated and it has only one claw.

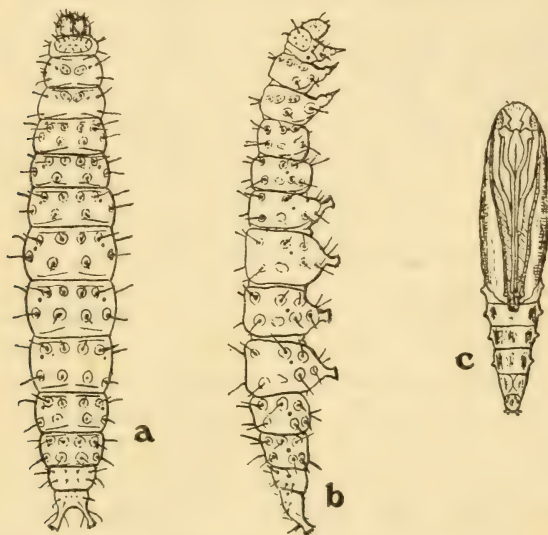


FIG. 45.—*a*, Dorsal, and *b*, lateral view of Caterpillar of Diamond-back Moth (*Plutella cruciferarum*); *c*, pupa (ventral view).  $\times 6$ . From Carpenter (*Journ. Dept. Agr. Ireland*, I).

The abdomen of the caterpillar is composed of the ten segments usually recognisable in the hind body of an insect. In most caterpillars five of these (the third, fourth, fifth, sixth, and tenth) carry each a pair of short cylindrical prolegs armed with circles or crescents of spines; these prolegs are of value in regard to the caterpillar's special mode of life, as they enable the creature to cling to or crawl along



a twig or even a leaf-edge of its food-plant. The body-segments are still all much alike, the cuticle is usually thin and flexible, and the general aspect of the caterpillar may be described as worm-like; it is essentially a "creeping thing."

The newly hatched caterpillar is very small, but it feeds voraciously and grows quickly, passing through its successive stages and undergoing four or five moults before it attains its full size. The caterpillar in its last stage is enormous compared with what it was when it left the egg, but it does not differ in any essential feature of outward form. Head, body-segments, jaws, legs, and pro-legs appear after each moult much as they did before it, and at no stage of larval life is there any trace of outward wing-rudiments. This last feature is, as D. Sharp (1898) pointed out, by far the most important of the readily observable distinctive characters of the type of life-history illustrated by the transformation of the caterpillar into the butterfly; we have seen that in the growth of cockroaches, bugs, aphids, and cicads, there are evident wing-rudiments at an early stage of growth after hatching, and the same condition is found in the aquatic nymphs of stone-flies, may-flies, and dragon-flies. But in the development of the butterfly no trace of wings is apparent until the last larval cuticle has been shed and the pupa revealed; on the pupa (Fig. 45, *c*) the wings may readily be seen at either side of the body, so closely adpressed indeed that they do not stand out, but quite recognisable as to their shape, as are also the legs and feelers, elongate like those of the adult, and sometimes also the slender, flexible maxillae which will enable the butterfly to feed by suction, the biting mandibles of the caterpillar used for feeding on solid plant tissues having vanished.

The pupa, then, resembles the adult insect much more closely than the larva, and this can be seen more clearly than in the case of the butterfly if we study the pupa of a beetle (Fig. 47, *b*) or a bee. For in these insects the pupal wings and legs are not closely adherent to the body as in the "obtect" butterfly chrysalid, but stand out in the manner

characteristic of the "free" pupa, as such a type is called. The obvious presence, when the pupa is revealed, of wings and other organs characteristic of the "imago" or perfect insect confirms our impression that the pupal stage of the life-history indicates a period of reconstruction and comparatively rapid change. But a knowledge of the processes of animal growth in general leads the student to infer that such profound changes could not be brought about without previous preparation. So that we are led to expect that wing-rudiments must be somewhere present in the cater-

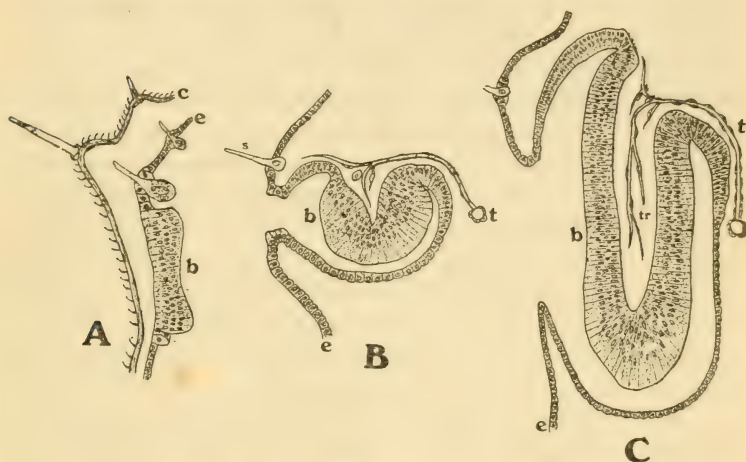


FIG. 46.—A, B, C, Stages in development of wing-bud (*b*) of a Lady-bird Beetle (*Hippodamia*), shown in section. *c*, cuticle (shown in A only); *e*, epidermis; *s*, sensory hair-cell; *t*, trachea; *tr*, tracheoles.  $\times 100$  (approx.). After Comstock and Needham, "Wings of Insects."

pillar or other insect larva. They were indeed observed more than a century and a half ago when P. Lyonet in his great treatise (1762) on the caterpillar of the "Goat" Moth (*Cossus*) saw two pairs of small white bodies lying in the fatty tissue of the second and third thoracic segments. He did not certainly recognise them as wing-rudiments, but he pointed out that their number and position suggested that such might be their nature. They are indeed the wing-buds of the insect, lying hidden beneath the body-

wall. These "imaginal discs" as they are now called, have been detected in all metamorphic insects whose development has been carefully traced. J. Gonin, for example, has shown (1894) that in the White Cabbage Butterfly (*Pieris*) they arise as thickenings beneath the skin, and grow inwards as they increase in size in such a way as to form little flattened hollow pads lying in thin-walled pouches continuous with the skin whence they originate; thus, although they are situated within the body, they retain their primitive connection with its outer wall. Branches from the air-tube system grow into them, prefiguring the main features of the nervures in the developed wing. After the last larval cuticle has separated from the skin in preparation for the final moult of the caterpillar, these wing-buds grow very quickly and are thrust out from their pouches; thus projecting from the surface they become covered with cuticle, and so the wings are apparent when, the moult completed, the pupa is revealed. A similar mode of wing-growth has been traced in the larva of a Lady-bird Beetle (*Hippodamia*) by Comstock and Needham (1899), some of whose drawings are reproduced here (Fig. 46). Wing-buds of essentially the same type can be demonstrated in the grub of the Honey Bee (Fig. 50, *f*, *h*).

Not only the wings, but all the organs of the winged adult that become apparent in the pupa, arise in the larva as imaginal discs, often sinking within the body but remaining connected by strands of tissue with the skin whence they first develop. Up to the third larval stage the leg of a caterpillar may be cut off without damage to the corresponding limb of the adult, but if such mutilation be perpetrated later in the course of development, the tip of the shin and the foot of the imaginal leg will be removed, as these then project into the cavity of the larval leg, though the basal region of the limb is sunk in a lateral depression of the body. The transformation of the internal organs differs in nature and degree in the various systems of organs and in the various orders of insects. Generally it may be stated that the nervous system, the heart, and the ovaries



or testes of the adult arise directly from the corresponding structures present in the larva with changes as to size and elongation, as well as separation or fusion of segmental structures such as nerve-ganglia. On the other hand, the digestive system and associated structures undergo dissolution at the close of the last larval stage and the corresponding organs of the winged adult are developed from special imaginal cells, which may be recognised during larval life, either appearing as small scattered units among the larger normal cells of the larval digestive epithelium, or forming aggregated groups at definite regions of the larval food-canal. Such small imaginal groups of cells, relatively few in number, give rise to the greater part of the internal organs of the adult, so that these organs may be regarded as new formations during early pupal life, while the larval structures, now no longer needed, are broken down by the chemical action of special enzymes, the effete products of the dissolution process being devoured by active, wandering "amoeboid" cells like white blood-corpuscles. This destructive process is known as "histolysis," and the replacement due to the growth of the imaginal discs as "histogenesis." For a detailed account and discussion of these processes reference may be made to the treatise of L. F. Henneguy (1904). The muscles and the air-tubes also undergo, like the digestive system, dissolution and reconstruction more or less profound according as these systems in the imago differ from those in the larva. The tissue of the larval fat-body serves as a reservoir of food-material which is drawn upon for the energy needed in the rapid processes of growth and change that go on at the crisis of transformation in the insect's life-history. These internal changes, the nature of which were in part elucidated by the work of A. Weismann (1864) on the metamorphosis of flies, and have been traced in full detail by subsequent students, are no less surprising than the changes in outward form which led some of the earlier naturalists to regard the formation of the pupa and the subsequent emergence therefrom of the winged adult as a veritable new birth. All the

various imaginal rudiments, however, are formed from organs or from groups of cells in the larva whose tissues have arisen from the segmenting egg in the course of embryonic development. The comparison of a pupa to a "second egg" is therefore fanciful, and the life-history of the butterfly or bee after hatching must be regarded as a specialised and curiously modified form of growth. In all such insects the hidden development of the wing-buds, lying apparently within the body, affords, as D. Sharp (1898) pointed out, a definite character by which these metamorphic or holometabolous insects (Endopterygota) may be separated from those hemimetabolous insects, undergoing little or comparatively slight transformation and exhibiting outward wing-rudiments early in their life-history (Exopterygota). We find here the essential distinction between "incomplete" and "complete" metamorphosis among insects.

The comparison of a butterfly with its caterpillar demonstrates that the adult insect or imago differs from its larva not only in structure but also in its manner of life, and this aspect of the study of insect transformation appeals to those interested in questions of life-relations and the organism's adaptations to meet the conditions under which it has to exist. The winged adult flies while the larva crawls; the butterfly sucks nectar from flowers while the caterpillar eats solid pieces of plant tissue, leaves, roots, or wood, which it bites off with its strong mandibles. As the student of the biology of insects reviews a series of larvae belonging to various types, he becomes convinced that in each case the form of the larva is adapted to its habitation and manner of feeding; its differences from the adult correspond with different life-relations.

It has already been pointed out that although the caterpillar differs markedly in aspect from its parent butterfly, its body is built essentially on the same general plan. There is agreement in the number of segments, in the regions (head, thorax, and abdomen) into which they are grouped, in the relative positions of the various systems of organs. The difference between a newly-hatched caterpillar and a

butterfly may easily be exaggerated. It is necessary to remember that such a young insect, rightly called a larva because in it the aspect of the adult is to a considerable extent masked, must not be regarded as an embryo hatched before its time. It presents, for example, a great advance in its stage of development on the young larvae of many Crustacea (such as water-fleas, certain shrimps, and crabs) in which there are but a few segments and limbs apparent,

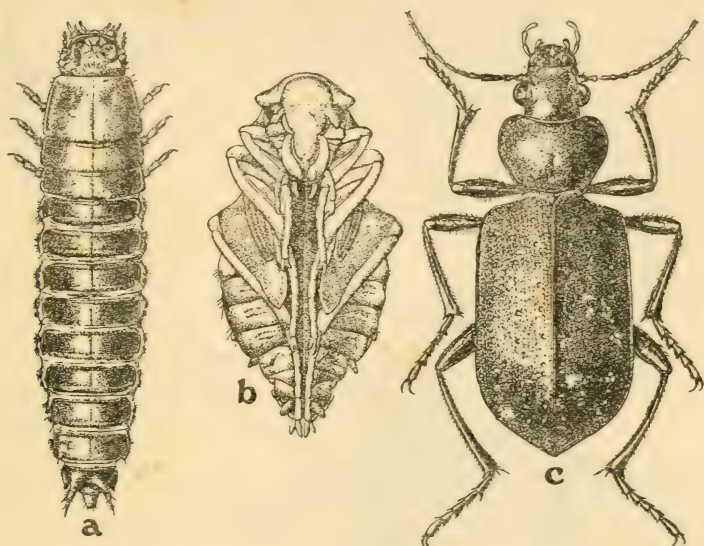


FIG. 47.—*c*, Ground-beetle (*Chlaenius bioculatus*), India. *a*, larva; *b*, pupa.  $\times 5$ . From T. B. Fletcher (*Bull.* 89, *Agr. Res. Inst. Pusa*, 1919).

the greater number of these appearing only after hatching. Still more does it display a contrast to the early larvae of starfishes and their allies, which are veritable precociously hatched embryos, comparable at most to those earliest stages in the development of insects that follow the segmentation of the egg.

Study of a series of grubs belonging to different orders of insects, or even to members of the single order of beetles (Coleoptera), furnishes examples of larvae some of which



differ from their adults less than a caterpillar differs from a butterfly while others differ much more. The grub of a ground-beetle (*Chlaenius*), Fig. 47, has the terga of the segments strongly chitinised so that the body is well armoured, and its feelers and legs are relatively long, while



FIG. 48.—Chafer (*Anomala bengalensis*), India. *a*, larva (side view); *b*, female.  $\times 3$ . From T. B. Fletcher (*Bull.* 89, *Agr. Res. Inst. Pusa*, 1919).

the mandibles are powerful and provided with strong sharp teeth; such a grub feeds, like its parent beetle, on weaker insects which it captures and devours. The well-known "wireworm," or larva of a click-beetle (*Agriotes*), has also a strongly armoured body; it is, however, narrow and

elongate with very short legs adapted for working its way through the soil where it spends its relatively long life of two or three years feeding on roots of plants. A chafer grub (Fig. 48) also feeds on roots, but does not wander as the wireworm does; only its head and its relatively long legs are firmly chitinised, the cuticle of the body-segments remains pale and flexible, the tail region being somewhat swollen, so that the grub looks like a fat caterpillar without pro-legs. It spends much time resting in an earthen chamber some distance underground feeding on adjacent roots. The larvae of beetles of the "death-watch" group

(Anobium, etc.) live and feed in tunnels which they make in wood, or among stored dried food-materials; they resemble somewhat miniature chafer-grubs, but their heads are smaller and their legs much shorter. From these we

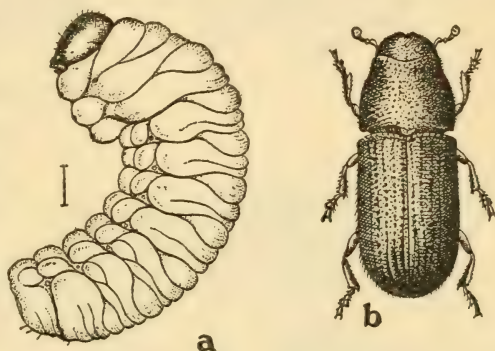


FIG. 49.—Pine Bark-beetle (*Dendroctonus brevicornis*), North America. *a*, larva (side view); *b*, male.  $\times 9$ . From J. L. Webb (*U.S.D.A. Ent. Bull.* 58, 1906).

pass naturally to the larvae of weevils (Curculionidae) and bark-beetles (Scolytidae), Fig. 49, in which the body-cuticle is white, flexible, and wrinkled, while legs are altogether wanting; such grubs live in concealed situations in the soil, or in plant tissues, mining leaves or timber, or in galleries beneath the bark. These larvae clearly differ from their parent-beetles more than a caterpillar differs from a butterfly.

Other orders of insects show still greater divergence between larva and imago. A wasp or bee-grub (Fig. 50) is legless and pale like a weevil's, but its cuticle is smoother and more delicate and its head much smaller.

Among the two-winged flies (Diptera) all the larvae are destitute of true legs, and in the house-fly and bluebottle group (Muscoidea) the head-region becomes so much

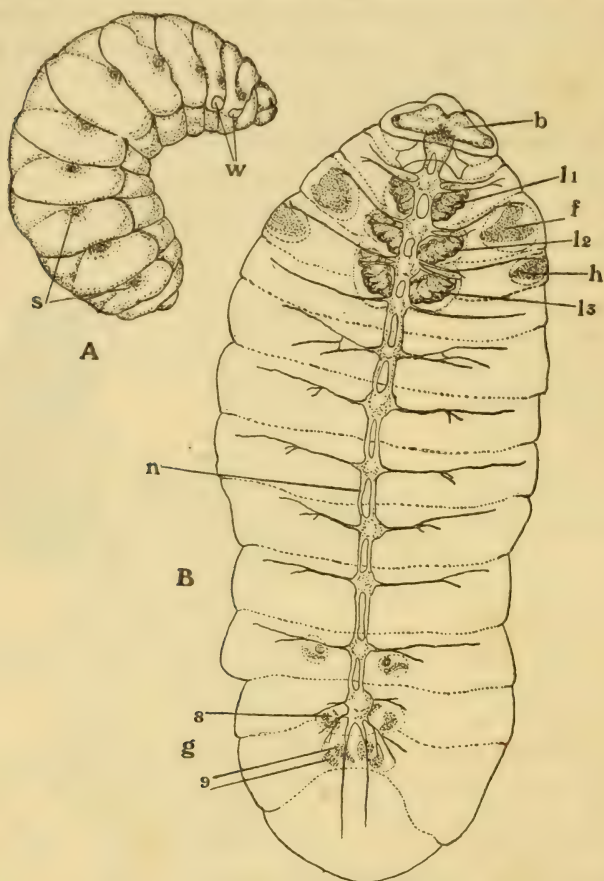


FIG. 50.—Larva of Honey Bee (*Apis mellifica*). A, side view,  $\times 4$ ; *w*, wing-buds seen through skin; *s*, spiracles. B, ventral body-wall with nerve-cord (*n*) exposed by dissection,  $\times 12$ ; *b*, brain; *l*<sub>1</sub>, *l*<sub>2</sub>, *l*<sub>3</sub>, imaginal buds of legs, *f*, forewing and *h*, hindwing buds, in their pouches; *g*, 8, 9, developing gonapophyses (processes of ovipositor). After J. A. Nelson (*Journ. Agr. Res. U.S.D.A.* xxviii, 1924).

reduced as to be hardly recognisable. The maggot (Fig. 51) of such a fly tapers from the broad tail to the narrow



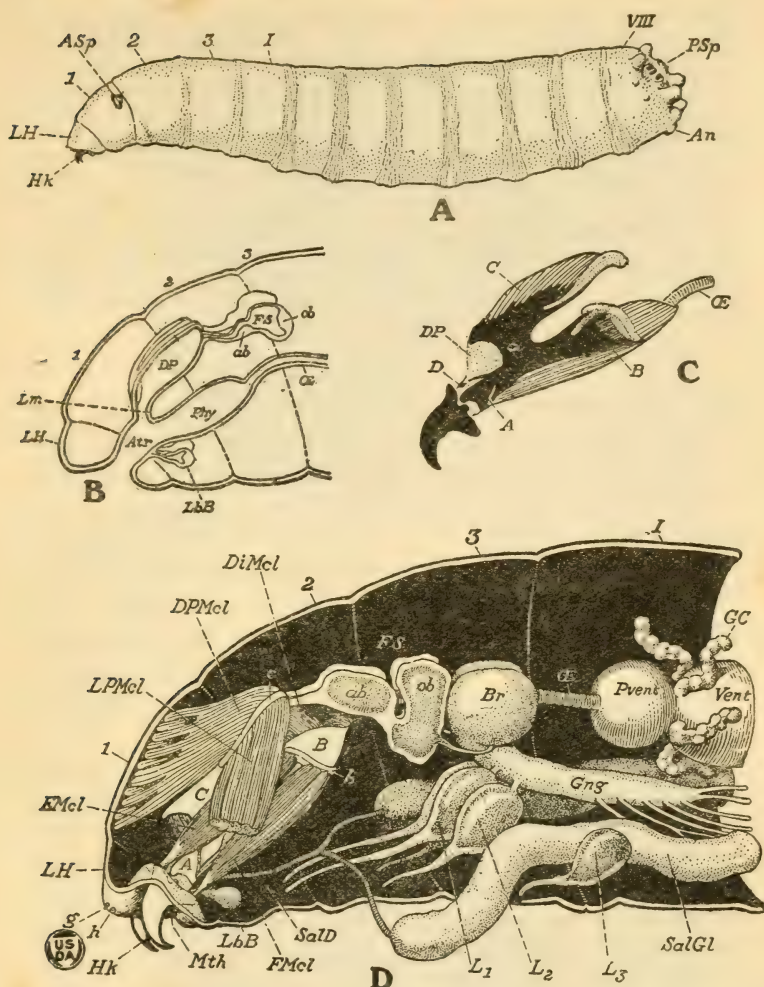


FIG. 51.—Larva ("Apple Maggot") of Trypetid Fly (*Ragoletis pomonella*). A, lateral view,  $\times 10$ ; B, diagrammatic longitudinal section through anterior region; C, pharynx and mouth-hooks, lateral view,  $\times 30$ ; D, section through anterior region of maggot,  $\times 30$ . 1, prothorax; 2, mesothorax; 3, metathorax; I, first abdominal segment; VIII, eighth abdominal segment; A, anterior lateral plate of pharyngeal skeleton; ab, antennal bud in frontal sac; An, anus; ASp, anterior spiracle; Atr, atrium, anterior, part of larval pharynx resulting from involution of original head of larva; B, posterior lateral plate of pharyngeal skeleton; Br, brain; C, dorsal or wing plates of pharyngeal

skeleton; *c*, ridge on plate *C* of pharyngeal skeleton; *D*, bridge plate of pharyngeal skeleton in roof of atrium; *DiMcl*, dilator muscles of pharynx; *DP*, dorsal pouch of atrium, divided beyond base into two wings containing plates *C* of pharyngeal skeleton and leading to roots of frontal sacs; *DPMcl*, dorsal protractor muscles of pharynx; *EMcl*, extensor muscles of oral hooks; *FMcl*, flexor muscle of oral hook; *FS*, frontal sacs, containing imaginal buds of antennae and compound eyes; *GC*, gastric caecum; *Gng*, ventral ganglionic nerve mass; *g*, *h*, sensory papillae of snout of larval head; *Hk*, mouth-hooks; *L<sub>1</sub>*, *L<sub>2</sub>*, *L<sub>3</sub>*, leg buds; *LbB*, imaginal buds of labium; *LH*, larval head; *LM*, labrum; *LPMcl*, lateral protractor muscles of pharynx; *Mth*, larval mouth; *ob*, imaginal bud of compound eye; *OE*, gullet; *Phy*, lumen of larval pharynx; *PSp*, posterior spiracle; *Pvent*, proventriculus; *SalD*, salivary duct; *SalGl*, salivary gland; *Vent*, stomach. From R. E. Snodgrass (*Journ. Agr. Res. U.S.D.A.* xxviii, 1924).

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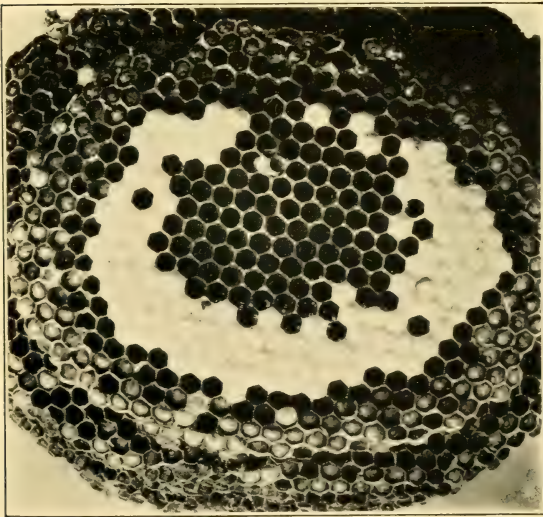
front end, where there are paired sensory tubercles, and strong mouth-hooks used for tearing, which can only with much doubt be compared with typical insect mandibles. An interesting peculiarity of the muscoid maggots is the restriction of spiracles to a large pair at the tail-end of the body and a small pair on the prothorax which can have but a very restricted function (Fig. 51, *PSp*, *ASp*). In some of these maggots several pairs of the lateral spiracles have been detected in a vestigial condition, their connecting air-tubes excessively slender and solidified by internal deposition of cuticle.

These larvae of wasps, bees, and muscoid flies, which differ—especially the last—so profoundly from their parents, are adapted each to its characteristic mode of life. The wasp-grub rests in its paper chamber (Plate VII) in the nest where it is fed on insect-fragments by its sisters the worker-wasps, and the bee-grubs in the waxen chambers of the comb are provided by the worker-bees with floral food materials such as honey and pollen. The soft defenceless cuticle, the small head and relatively weak jaws are enough for creatures that are protected and provided for, have no need to flee from enemies nor to wander in search of food. A remarkable feature of these hymenopterous grubs is that throughout the larval stages the hind intestine is closed and no waste matter passes from the food-canal until just before pupation; this seems a suitable adaptation in view

PLATE VII



NEST OF TREE-WASP (*Vespa norvegica*). Envelope partly cut away.  
One-sixth size.



COMB OF WASP-NEST (*V. vulgaris*), seen from below. One-third size.  
*To face p. 182.* [H. Britten, photo.]





of the highly nutritious food of these grubs and their prolonged period of residence in a crowded nest or hive. Similarly the muscoid maggot, with its front region tapering towards the head armed with strong mouth-hooks, is excellently adapted for burrowing into the mass of its foodstuff—the bluebottle's larva, for example, into soft flesh, the house-fly's into horse-dung or garden refuse, the cabbage-root fly's or the mangel fly's into its appropriate plant-tissue; and in many cases it is easy to recognise the advantage of restricting the functional spiracles to a pair of large ones at the tail-end which remains nearest to the free surface of the food-mass within which most of the maggot's body is buried. In the larvae of several groups of flies such as the gnats (*Culicidae*) and the drone-flies (*Eristalis*) these tail spiracles are found at the end of a very short or elongate hinder outgrowth of the body, enabling the grubs, which live under water, to obtain contact with the atmosphere through the surface-film and thus breathe the upper air while they feed in a ditch or puddle which is possibly most foul.

The study of such a series of insect-larvae as we have rapidly passed in review brings out clearly the striking adaptation of each to its own manner of life during the period of immaturity and growth. It also suggests that the adaptations have been brought about by the divergence in a less or greater degree of each larva from the form and conditions of its parent. Those young insects such as grasshoppers, cockroaches, and bugs, which resemble their parents closely in form, usually live in the same surroundings as the adult and on the same kind of food. The fact of larval adaptation to special life-conditions in conjunction with the fact that an insect-larva's structure is comparable with that of an adult rather than with that of an embryo, suggests most strongly that the creatures during the early stages of their life-history have diverged from the primitive parental type, in many cases by degeneration, while the adults have diverged by specialisation and elaboration. This view is confirmed by consideration of our series of

young insects, which clearly illustrates increase in divergence of larva from imago. It also helps to explain that feature of insect metamorphosis according to which the transformation becomes most profound in the most highly specialised groups. It is well known that among animals generally, marked transformation in the course of the life-history characterises creatures of comparatively primitive organisation, which live in the sea and as a rule produce eggs of small size. This combination is illustrated by the profound transformations undergone by starfishes and other echinoderms, or by the marked change of form in growth after hatching to be observed in most fishes, compared with the young of terrestrial reptiles and birds hatched from large-yolked eggs in a condition already well-developed. Insects form a class of creatures essentially terrestrial and aerial, whose eggs are of relatively large size. Yet the young of most insects pass through marked changes after hatching and the greatest degree of change is shown by members of the most highly specialised orders. From the facts surveyed in this chapter it will be apparent that the insect larva, even of a type so degraded as the muscoid maggot, is not a precociously hatched embryo, but a modification of the type of structure displayed by the developed insect. Whenever the larva differs markedly from the imago we find that it lives and feeds differently from the latter, and we conclude that there must have been specialisation not in one direction only, but in two. The imago shows high elaboration in the form of jaws, wings, sense-organs, while the larva, even if degenerate, is also itself specialised in correspondence with a mode of life widely divergent from that of the winged insect. The degree of divergence between the adult and the larval structure and life necessitates a corresponding degree of reconstruction at the crisis of development marked by the pupal stage, involving a resting period in the life-history during which the reconstructive processes can be carried out.

In the series of grubs, belonging to beetles and other insects, illustrating increasing divergence between larva and



imago we noticed (pp. 177-8) that there is a type of larva with cuticle predominantly firm so that the body is well armoured and provided with relatively long feelers and legs. When such a larva is slender in build and furnished with a

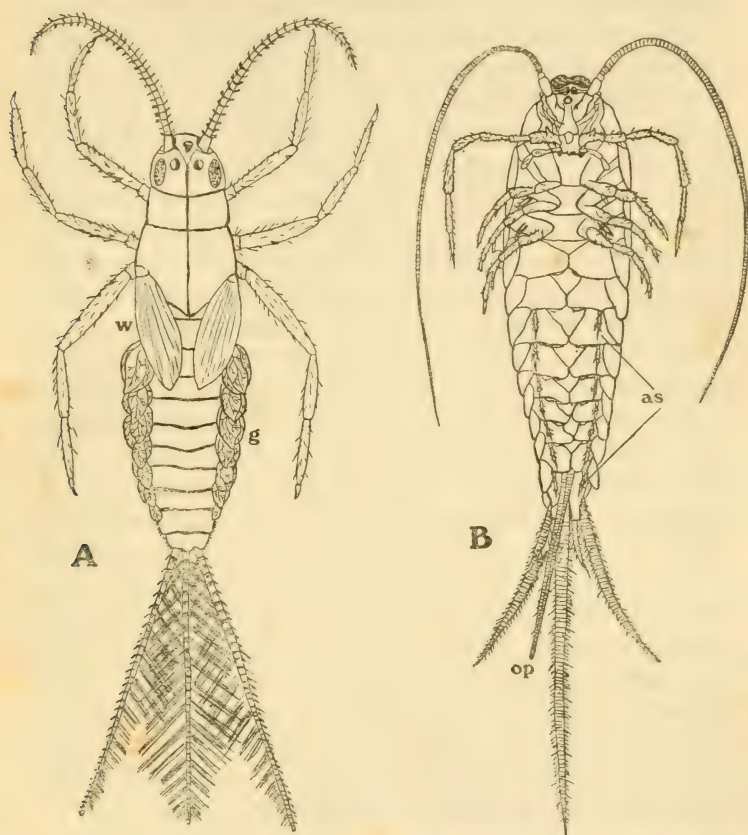


FIG. 52.—A, Nymph of Mayfly (*Chloeopsis diptera*), *w*, wing rudiments; *g*, abdominal gills.  $\times 8$ . After Vayssière and Eaton. B, Bristle-tail (*Petrobius maritimus*), female (ventral view), *as*, abdominal stylets; *op*, ovipositor.  $\times 5$ . In part after J. T. Oudemans.

pair of tail appendages (cerci), as in the familiar mayfly nymph (Fig. 52, A), it presents, as F. Brauer (1869) pointed out, rather strong likeness to a bristle-tail (Thysanuran) such as a Machilid (Fig. 52, B) or Campodea, hence it is

often distinguished as a "campodeiform" larva. As the wingless bristle-tails are the most primitive of living insects, it has been suggested that the campodeiform is the primitive type of insect larva, and that larvae such as caterpillars or chafer-grubs—the "eruciform" type of A. S. Packard (1898)—are to be regarded as more strongly modified in correlation with their habits, which differ more markedly from those of their adults. In the maggot of a muscoid fly we see a still more profoundly modified, in fact degraded, "vermiform" type of larva. Confirmation of the opinion that these types indicate an increasing degree of divergence between larva and imago, is afforded by those insect life-histories which exhibit more than one larval type in the course of development. For example, the young of many oil and blister beetles are hatched from the egg as tiny active, armoured campodeiform larvae which seek to attach themselves to the body of a bee, and if successful, are carried to the nest, where, after the first moult, they become changed to soft-coated grubs feeding on the stored honey. The campodeiform precedes the eruciform type in the one life-history, and the inference is drawn that the former condition is exceptionally retained because the parent beetle cannot enter the bee's nest so as to lay her eggs where the grubs will spend the greater part of their term of existence, and the active long-legged, armoured form of larva is the best adapted for making its way thither. In the case of the vast majority of metamorphic insects which place their eggs upon, within, or adjacent to the material whereon their grubs will feed, the young insect, as soon as hatched, conforms to the eruciform or the vermiform type.

These considerations throw light on the nature of the primitive immature insect and on the problem of the origin of the more specialised and degraded larval types. It may now be advisable to pass to another problem which confronts the student of insect development: the relation of the open (exopterygote) to the hidden (endopterygote) manner of wing-growth. We have seen that the former is

characteristic of the more generalised and the latter of the more specialised orders of winged insects. From this, as well as from the probability that there has been mutual divergence between larva and imago among the metamorphic insects, it may be presumed that the hidden method of wing-growth has in these orders superseded the primitive open method. It is by no means easy, however, to understand why the wing-rudiments which are evident on the outer aspect of a young grasshopper early in its life-history, do not in a beetle or moth pupa become externally visible until the last larval cuticle has been shed and the pupa revealed. We have seen, from the origin and growth of the imaginal wing-buds in a caterpillar, how this state of things is brought about; the problem that confronts the student is to find a reason why they sink into apparently internal pouches instead of growing outwards. The fact that they grow outwardly in the more primitive orders of insects indicates that the hidden type of growth must be regarded as secondary; the problem may therefore be stated as the mode of derivation of the one type of wing-growth from the other, the origin of the endopterygote from the exopterygote life-history.

In elucidation of this problem it may be instructive to notice examples of the abnormal appearance of outward wing-rudiments on the larvae of certain metamorphic insects. This was observed in "mealworms," grubs of the beetle *Tenebrio molitor*, by R. Heymons (1896), and has recently been studied with some detail in that same species by H. Singh-Pruthi (1924). Abnormal outward wing-rudiments on mealworms (Fig. 53) have been usually noticed on well-grown specimens, but Singh-Pruthi has demonstrated them on comparatively early larvae and has shown that their appearance is facilitated by submitting the insects to a high temperature, which has the effect of retarding or preventing the final transformation into beetles. Most of these abnormal mealworms fail to pupate; the pupae that do result are also abnormal, and those individuals that succeed in reaching the pupal stage rarely develop into beetles.



Apparently these abnormal insects at all stages experience a difficulty in shedding the cuticle: "Sometimes . . . an individual resembles neither a pupa nor a larva, as it has the head and thorax of the former and the abdomen of the latter." A fact of much interest discovered by Singh-Pruthi is that in the abnormal mealworms only a part of the wing-rudiment is external; the remainder lies as usual within

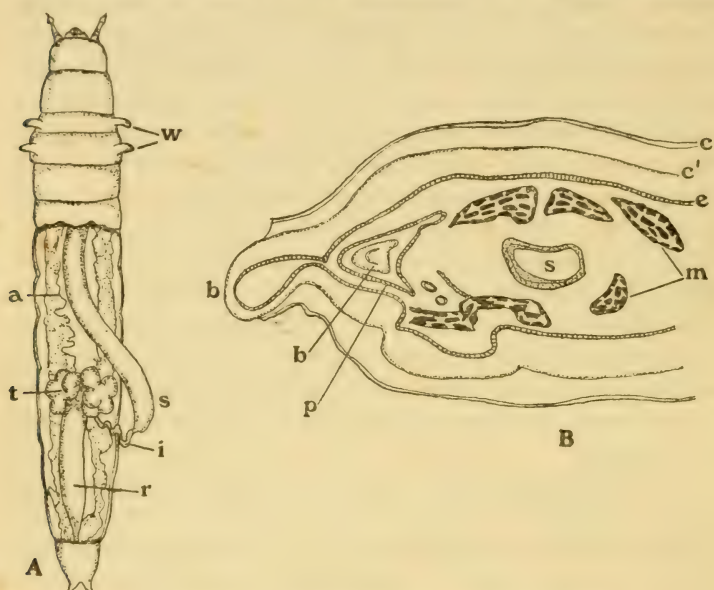


FIG. 53.—A, Mealworm (Larva of *Tenebrio molitor*), with abnormal external wing-rudiments (*w*), partly dissected to expose food-canal (*s*, stomach; *i*, intestine; *r*, rectum); *a*, fat-body; *t*, testis.  $\times 3$ . B, Transverse section through thorax.  $\times 20$ . *e*, epidermis; *c*, *c'*, old and new cuticle; *s*, stomach; *m*, muscles; *b*, wing-rudiment, part external and part in pouch (*p*). After H. Singh-Pruthi (*Proc. Camb. Phil. Soc. Biol.* i, 1924).

the inpushed pouch of the skin (Fig. 53, B, *p*). This indicates that a portion only of the wing-bud was everted during the preparation for the preceding moult. During the last twenty years somewhat similar observations have been made on the larvae of other beetles and of certain moths; of these the most noteworthy is the case of the ground-beetle *Lebia*

*scapularis* described by F. Silvestri (1905), who considers that in this species the final larva with external wing-rudiments is a normal prepupal stage in the life-history. The outward appearance of part of a wing-rudiment on the thoracic segment of a beetle or other metamorphic insect may be most reasonably interpreted as a reversion towards the primitive condition found in young exopterygote insects, indicating that from such conditions the metamorphosis has been elaborated by the postponement of the outward appearance of the wing-buds until successively later stages of the life-history. This postponement is clearly correlated with the structural divergence between larva and imago to which reference has already been made.

It has also been noted that such divergence is commonly associated with difference in feeding-habits. Comparison of larva and imago from this point of view furnishes an interesting and instructive study. Among beetles and the Alderfly group of the Neuroptera, the larva as well as the imago bites solid food by means of typical insectan mandibles ; in the details of its feeding, however, the larva usually differs from the adult, devouring roots, for example, while the latter eats leaves, or during its life in pond or stream pursuing aquatic prey while the perfect insect attacks inhabitants of the land and air weaker than itself. In most families of Neuroptera as well as the carnivorous Water-beetles (Dyticidae) the perfect insect has normal biting mandibles, while in the larva the slender curved jaws are modified for piercing the bodies of insects which serve as prey and sucking their juices. The very remarkable divergence as regards feeding shown by the Lepidoptera, among which the caterpillar has strong biting mandibles, while butterflies and nearly all moths have vestigial mandibles and elongate flexible maxillae adapted for sucking nectar or other fluid, is familiar to all students of insect life. In connection with our contention as to the mutual divergence of imago and larva among metamorphic insects it is noteworthy that the Micropterygidae, the most primitive of all moths, have still, when adult, small functional mandibles,

while their maxillae retain the typical form with slight modification, the lacinia or blade, absent in Lepidoptera generally, being well developed.

The contrasts in feeding habit between insects of the same kind during the immature and adult periods of their lives suggests the mention of the still greater contrast afforded by many insects which do not feed at all after completing their transformations and acquiring their wings. In most insect life-histories the preparatory stages extend over a far longer time than the duration of adult life. Dragon-fly larvae often spend several years under water before emerging into the air in readiness for the winged insect's flight of a few weeks or months, while the underground life of the cicad already mentioned in this chapter is prolonged for thirteen or seventeen years, the winged adult dying before the winter of the year in which it comes up. In most metamorphic insects with a yearly life-cycle the life of the imago is much shorter than that of the larva, the former to be reckoned usually in weeks and the latter in months. We have seen that the larval period of the life-history affords an opportunity for eating and digesting food and storing it up in the tissues, so that there may be ample supply for the extensive re-making of the creature at the pupal period. Apart from the exceptional precocious modes of reproduction to be considered later in this chapter, pairing and egg-laying are unknown until the insect has reached its adult condition, so that the imago may be regarded as essentially performing the function of reproduction. It is not surprising, therefore, from this point of view to find that in a number of insects—whether exopterygote as the Mayflies, or endopterygote as the Silkworm Moths (*Bombycidae* and *Saturniidae*) and the botflies (*Oestridae*)—the imago when developed has the jaws so excessively reduced that it is incapable of taking food, and its activity is entirely concerned with breeding, the feeding necessary for the accomplishment of its life-purpose having already been performed during the larval stages. It has often been remarked that the power of flight, acquired by



the vast majority of insects when adult, has an important if indirect bearing on reproduction, as it facilitates a wide range over localities suitable for egg-laying, and thus tends to bring about an increase of the area occupied by the species.

It has been noticed that in the growth of insects generally there is something of a crisis at the penultimate stage of the life-history, and this becomes especially evident in the development of those insects, the vast majority of the class, that undergo complete transformation with a resting pupal stage between the end of the larval and the beginning of the adult life. The nature and meaning of the pupa has always presented a fascinating problem to students of the biology of insects. The Greek philosopher Aristotle regarded the insect pupa as a second egg, and William Harvey (1666), taking a similar view, suggested that the amount of food-material in a butterfly's egg is insufficient for the building up of so highly organised a being as the parent, and so only the imperfect caterpillar can be hatched from it; the caterpillar after weeks of feeding stores up the necessary amount of food and then reverts to the condition of a second egg (the pupa), whence the butterfly in due time may be hatched.

A superficial examination of the hard, egg-shaped puparium of a bluebottle or the brittle cocoon wherein rests the pupa of an "egg" moth might be thought to afford countenance to such a view. But even in the obtect pupa of a butterfly, with its wings and appendages closely adherent to the body, many of the organs of the perfect insect can be clearly recognised, and much more is this the case in the "free" pupa of a beetle, lacewing, or wasp, in which the wings and limbs stand out from the body in much the same way as they do in the adult. The envelope of the actual pupa, therefore, is clearly the cuticle of the insect itself, even though, in the case of an obtect pupa, it is specially modified in correspondence with what is predominantly a passive stage in the life-history.

Examples have already been given of exopterygote insects such as cicads, and scale-insects, in which the penultimate

instar is quiescent, and in the transformation of the last-named family we notice that the wing-rudiments of the male are formed beneath the preceding larval cuticle. These conditions suggest an approach on the part of certain Exopterygota towards the pupa of metamorphic insects. The Mayflies (Ephemeroptera) are of especial interest in this connection because they combine the open method of wing-growth with a very wide divergence between larva and imago. The larval mayfly (Fig. 52, A) might almost be described as a bristle-tail adapted for aquatic life, since in its long feelers and tail-cercopods and its crustacean mandibles, it closely resembles a thysanure, while its paired abdominal tracheal gills must be compared, as R. Heymons (1896) and C. Börner (1909) have shown, with a bristle-tail's short abdominal limbs. There is a long aquatic larval life with very many moults, outward wing-rudiments becoming conspicuous in the later stages. The mayfly has little obvious likeness to its larva except in its elongate abdomen bearing terminal cercopds, for the feelers are very short and the mouth parts reduced to mere vestiges, so that the insect in its winged state cannot feed and its very name implies the rapid passing of its life. Its aerial existence nevertheless presents a feature of very great and exceptional interest. When the ripe nymph has come out of the water and shed its cuticle, the instar revealed, though possessing developed wings, is not the true adult, but a "sub-imago" which has to undergo another moult before the insect reaches the imaginal state and becomes capable of reproduction. In no other group of insects does a moult occur after the power of flight has been acquired. The existence of the mayfly's sub-imago suggests the fascinating idea that a moult after the development of functional wings was possibly of general occurrence among the primitive winged insects of past ages. In connection with this view it is worthy of notice that in many of the less specialised metamorphic insects of to-day—Coleoptera and Neuroptera, for example—the pupal wings are relatively of large size, and that in the transformation of several Hymenoptera, including

the familiar hive-bee, the casting of the last larval cuticle, whereby a "prepupa" with conspicuous wing-rudiments

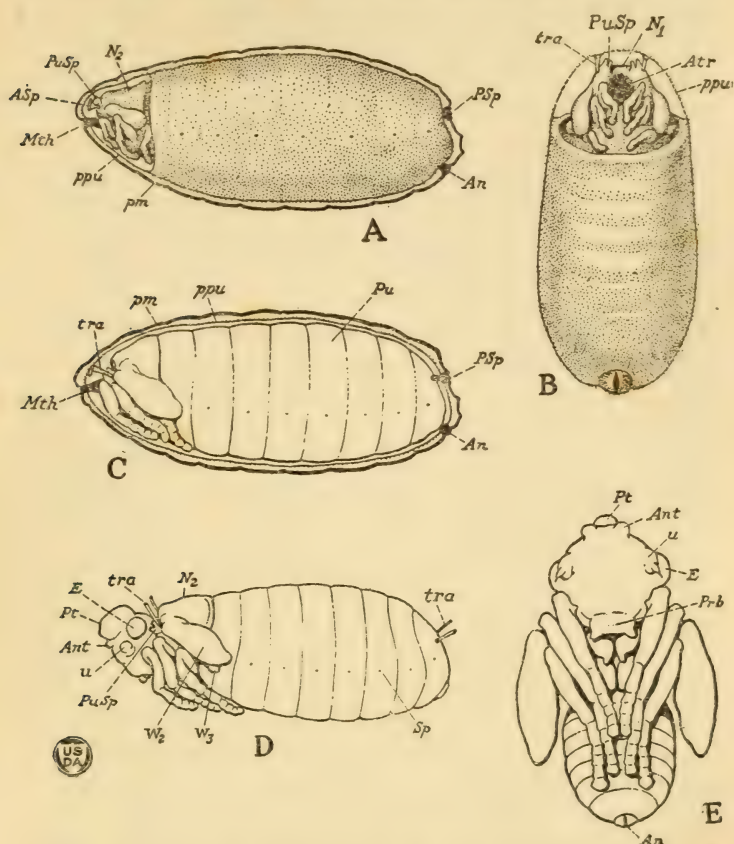


FIG. 54.—Pupa and Puparium of *Rhagoletis pomonella*.  $\times 10$ . A, early-stage pupa enclosed in puparium and shedding prepupal cuticle (lateral view); B, the same, ventral view; C, later pupa within puparium and separated prepupal cuticle (lateral view); D, still later pupa removed from puparium (lateral view); E, pupa shortly before emergence (ventral view). An, anus; Ant, antennal lobes; ASp, anterior larval spiracle; Atr, atrium (anterior part of larval pharynx); E, compound eye; Mth, larval mouth;  $N_1$ , pronotum;  $N_2$ , mesonotum; pm, puparium; ppu, prepupal larva (fourth larval instar, inside of puparium); PSp, posterior larval spiracle; Pt, ptilinum; Pu, pupa; PuSp, pupal dorsal spiracle of pronotum; tra, tracheal linings of preceding instar; u, subocular lobe;  $W_2$ , wing;  $W_3$ , halter.  $\times 10$ . From R. E. Snodgrass (*Journ. Agr. Res.*, U.S.D.A. xxviii, 1924).



is revealed, is followed by another moult ushering in what is regarded as the true pupal stage. R. E. Snodgrass (1924) has described in the small muscoid dipteran *Rhagoletis*, a "prepupal" cuticle which is formed within the puparium and envelops the pupa (Fig. 54). This instar, however, resembles the contracted maggot in form and has no wing-rudiments.

Further, in connection with the biology of the pupa, it is noteworthy that among the metamorphic insects there is a great range of variation in the creature's power of movement during this stage of its life. The house-fly pupa lies quiescent within its hard protective puparium—the shrunken and condensed larval cuticle—out of which the fly has to make its way after emerging from the cast pupal coat. The pupa of a butterfly or of a moth belonging to one of the highly organised families can move only a few of its abdominal segments. But among the more primitive Lepidoptera the pupa, provided with rows of locomotor spines on its abdominal segments, works its way partially out of its cocoon or from the earth in which it lay buried; the empty pupa coat of the Goat Moth (*Cossus*) may be seen partly protruding from a tree wherein the caterpillar fed, that of a Swift Moth (*Hepialus*) from the surface of the soil in which the larva devoured roots. Among the more primitive Diptera the same tendency to pupal activity may be noticed in cases where the life-conditions render it appropriate; the pupa of a Crane-fly (*Tipula*) raises the front half of its body out of the ground, and gnat pupae swim actively through the water making use of the surface film to obtain atmospheric air for breathing by means of paired "trumpets" on the thoracic region of their bodies.

From the foregoing examples it may be realised that while insects practising the open method of wing-growth are as a rule active, and those practising the hidden method passive in the penultimate stage, there is no absolute deviation in this respect between the two great types of insect life-history. The pupa or its corresponding instar seems

to display just as much activity as may correspond to its manner of life or to the necessity of preparation for the final moult. The details of structure and habit are largely adaptive, and the course of the life-history of insects as a whole suggests a great degree of plasticity in correspondence with biological relations.

The same conclusion as to a plasticity in the details of development and correspondence to environmental needs is suggested by many facts which confront the student as startling exceptions to the normal progress of insect transformation; some examples of such may fitly close this chapter.

Reference has already been made to the summer generations of greenfly (Aphids) in which the eggs develop within the mother's body so that the young are not hatched but born. Many two-winged flies (Diptera) give birth to active maggots instead of laying eggs. The Sheep-fly (*Oestrus ovis*), for example, usually deposits tiny larvae in the nostrils of the sheep, though sometimes according to the weather conditions, as W. E. Collinge (1906) has shown, she lays eggs, whence later the maggots are hatched. The big Flesh-fly (*Sarcophaga carnaria*) is constantly "larviparous," and so are many of the Tachinid flies whose maggots feed as parasites in the bodies of other insects. The female of a species of *Compsilura* is provided with a sharp "larvipositor" by means of which she pierces the body-wall of a caterpillar and thus places her offspring safely inside, where they invade the wall of the stomach and begin to feed. More rarely does the larva undergo most of its growth within its mother's body; the dreaded African Tsetse-flies (*Glossina*) as well as certain Dipterous insects (Hippoboscidae and Melophagidae) which suck blood from mammals and birds, bring forth mature larvae that pupate immediately after birth; hence these last named insects are often called "pupiparous." Some of these in correlation with their parasitic life are wingless, and there are two most remarkable types of wingless Diptera, living as "guests" in the nests of termites in the African and

Eastern tropics—known as *Termitoxenia* and *Termitomyia*—from whose life-history the whole larval and pupal stages are omitted, for according to their discoverer, E. Wasmann (1901), the former lays a relatively enormous egg whence a developed adult is hatched, while the latter gives birth to a single offspring already in the adult form. It is remarkable that such extreme abnormalities of life-history as these should occur among insects of that order (the *Diptera*) in which the ordinary course of transformation has become most elaborated with the most profound difference between adult and larva.

While in these insects the preparatory stages are largely or wholly omitted from the life-cycle, there are other *Diptera* in which young may be produced by larvae or pupae, so that insects not adult have the power of reproduction; these furnish examples of "paedogenesis" or precocious parenthood. More than half a century ago O. Grimm (1870) saw female pupae of the midge *Chironomus* lay eggs which gave rise to active larvae; we have seen that a typical insect pupa is closely like an adult in essential features of form, so this exceptional occurrence might be regarded as a somewhat surprising instance of virgin reproduction. Five years earlier, however, N. Wagner (1865) had noticed that within a grub of certain gall-midges (*Cecidomyidae*) a number of smaller larvae might be seen, these ultimately making their way out to free life through the body-wall of their larval mother. It is now known, as stated by W. Kahle (1908), that these abnormal young are developed from eggs which break loose from the ovaries already present in the parent larva, and float in the body-cavity, where they segment and form embryos, which develop into the larvae that burst out of the parent's body. After a succession of these larval families young are produced that complete their transformation into pupae and adults, so that the whole cycle is made up of a sexual generation alternating with a number of virgin larval generations such as is normal in several groups of animals, notably in certain parasitic worms.



Of all aberrant cases of insect development perhaps the most remarkable is the "polyembryony" of certain small

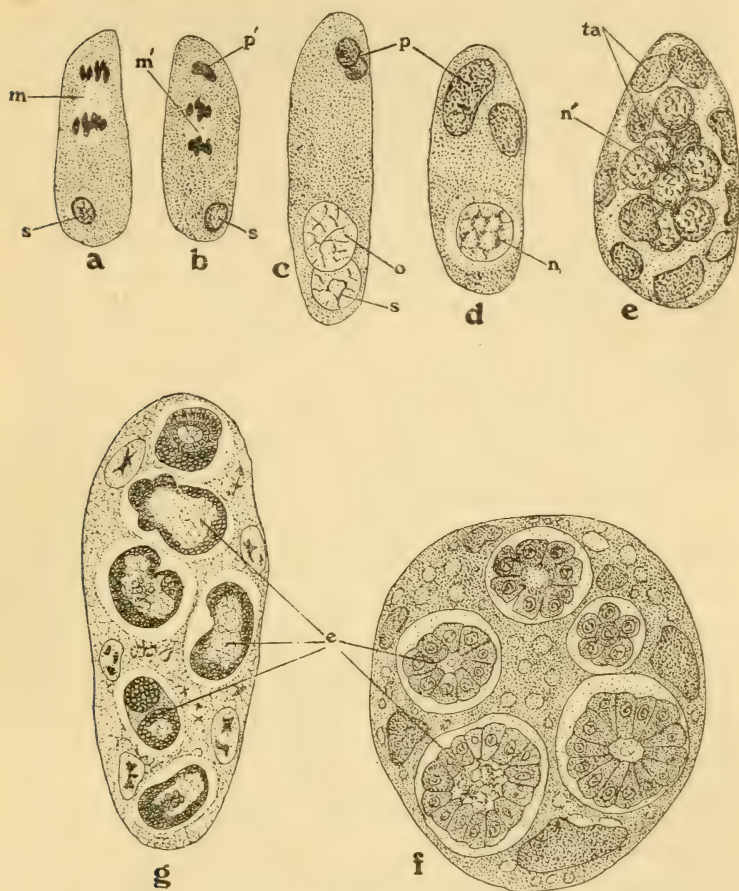


FIG. 55.—Polyembryonic development of *Platygaster vernalis*. *a, b*, egg undergoing maturation divisions (*m, m'*); *p'*, first polar body, *s*, sperm-nucleus; *c, d*, conjugation of egg and sperm nuclei (*o, s*) to form zygote nucleus (*n*); polar-bodies (*p*) increasing in size; *e*, later stage when the polar bodies have given rise to nutritive cells (*ta*) the trophamnion, surrounding the eight embryonic cells (*n'*), derived from the zygote-nucleus,  $\times 1350$ ; *f, g*, still later stages, with embryo (*e*) developing from each embryonic cell, *f*  $\times 700$ ; *g*  $\times 160$ . After R. W. Leiby and C. C. Hill (*Journ. Agr. Res.*, U.S.D.A. 1925.)

parasitic Hymenoptera. In this strange mode of development, as observed in *Encyrtus* of the Chalcid family by P. Marchal (1904), the female lays, in the egg of a moth, her minute egg so that it becomes enclosed in the body of the growing embryo as this develops into the caterpillar. The *Encyrtus* egg undergoes a curious kind of development, the polar nuclei persisting and multiplying at one end, while the egg nucleus, which may be fertilised or not, segments in the hinder region of the egg-substance and forms blastomeres. Ultimately the polar cells give rise to a nutrient capsule which spreads around the embryonic cells; these by a process akin to budding form a large number of embryos, in some cases over a hundred resulting from a single egg. Growth is slow during the winter while the host larva develops in the egg-shell, but after hatching, when the caterpillar begins to feed, the embryonic mass of the parasitic chalcid increases rapidly in size, and assumes the form of a sinuous thread extending through the caterpillar's fat-body, the nutrient membrane being now enclosed in a sheath derived from the host's tissues. At length the *Encyrtus* grubs become free in the caterpillar's body-cavity and finally eat their way out through its dried skin and cuticle to pupate and assume the adult form. Allied forms, which have been found to undergo a similar course of development, are described by F. Silvestri (1908) and R. W. Leiby (1922). The result is to bring about a hundredfold multiplication between the single egg laid in the egg of the moth by the tiny chalcid fly and the enormous family at the close of the completed transformation. R. W. Leiby and C. C. Hill (1923, 1924) have shown that in species of *Platygaster* (belonging to the Proctotrupidae), parasitic on gall-midge ("Hessian Fly") larvae, there may be the usual direct development of the egg into one larva, or a poly-embryonic development resulting in the production of six or eight parasitic grubs (Fig. 55). This condition, suitable to a host-larva of small size, suggests an early stage towards the abnormal fecundity of *Encyrtus*.

In face of such facts as these, the student cannot but feel

convinced that the various types of growth exhibited by various members of the class of insects are the result of modification and specialisation in the course of a long racial history, and that the creatures show at all stages of their growth an adaptive plasticity which may respond to changing conditions in ways that are strange and new.



## CHAPTER VIII

### FAMILY LIFE

IN the two preceding chapters we have sought to follow the processes of reproduction and growth among insects ; now we turn to consider the behaviour of the creatures in connection with these processes. The insect in its final winged condition has as its essential function the perpetuation of its race, and the activities of an adult insect are, to a great degree, obviously concerned with breeding in its various aspects. Pairing of the sexes is a necessary preliminary to the fertilisation of eggs, and the prospective mother must place her eggs in situations suitable for their development if the young are in their turn to grow to maturity. Her egg-laying may be her only and sufficient contribution to the welfare of these young, but not a few female insects feed or otherwise tend their offspring after hatching. In some cases the members of a family remain in association for a shorter or a longer period of larval life ; when the association is preserved after the adult condition has been attained, the family may be said to pass into a community and the life of such insects becomes definitely social.

The pairing of the sexes may naturally be considered first among the various activities concerned with reproduction and the rearing of the young, and of especial interest are certain aspects of behaviour preliminary to pairing, which may be regarded as comparable, at least in some degree, to the courtship practised by many back-boned animals. Insects have diverse ways of attracting members of their own kind but of the opposite sex. Some of these are clearly simple responses to sense stimulation,

while others involve behaviour that suggests selection or choice.

The recognition by an insect of a possible mate often depends upon the sense of sight. In a previous chapter (p. 90) evidence has been given that butterflies may be attracted when they see a wing of one of their own kind lying on the ground so that they stoop towards it. In most insect families it is the male that seeks the female, as is the case among animals generally, and the distinctive colour-pattern of the wings in such insects as butterflies apparently serves as an attraction when it is recognised. Occasionally the female is attracted by the male; this is the method of courtship in the Swift Moth *Hepialus humuli*, a species known as the "Ghost," because the male's wings are of a sheeny white above while the female's are, like those of both sexes in related species, brownish in hue. In the dusk of the midsummer evenings the white male hovers above the damp pasture or marsh-land; a female attracted by the white wings collides with him and the two then drop among the herbage and pair. It is of interest to notice that in the most northerly districts of its range, including Shetland, where at midsummer it is never really dark at night, the male *Hepialus humuli* is of the same brownish aspect as the female. The obvious conclusion is that the conspicuous white colour of the common British form is a special adaptation to aid courtship and hasten pairing; the male has become modified in correspondence with the special breeding habits of these insects. It is well known that in many butterflies of various families the male is adorned with bright colour while the female is comparatively plain; several of our British "Blues" (Lycaenidae) and the "Orange-Tip" (*Euchloe cardamines*) among the Pieridae afford examples of this. The characteristic blue colours of the male *Polyommatus icarus*, *Argiades corydon*, and *A. bellargus*, respectively, may be regarded as facilitating recognition by their several mates; but there is no convincing evidence that female butterflies or other insects choose their mates in a "brilliance competition," as suggested by C. Darwin (1871) in his well-

known theory of sexual selection. The actual pairing of butterflies usually takes place while the insects are in the air, and during the nuptial flight one partner carries the other, whose wings remain closed in the usual resting position, the upper surfaces meeting over the back. Darwin pointed out that, as a rule, the male butterfly carries the female, except in those exceptional cases where the latter sex is the more brightly coloured; then the female carries the male. This generalisation has been to a great extent confirmed by the extensive observations on tropical African insects made by G. D. Hale Carpenter (1920). A courting male butterfly often strokes the wings of a desired mate with his fore-feet; if his attractions prove ineffectual he flies away and leaves her, if she accepts his advances he carries her off. At least some of the females just mentioned as more brightly coloured than their mates, are more active than they in the courtship, so that examples are afforded of a complete reversal of the parts commonly played by the two sexes in the drama of pairing.

Dragon-flies, which vie with butterflies in the brilliance of their colours, comprise many species in which the male displays a brighter or more conspicuous appearance than his mate. Thus in our two common large British "damsel-flies," *Calopteryx virgo* and *C. splendens*, the wings of the female are uniformly russet or hyaline, while those of the males are respectively suffused with deep metallic blue, or each traversed by a broad dusky or blue patch. It is likely that such conspicuous distinctions may serve as recognition-marks to the females. In some dragonflies definite acts of courtship have been observed. R. J. Tillyard (1917) describes how in the small green Australian *Hemiphysalis mirabilis*, the abnormally long white terminal "inferior appendages" of the male "are displayed as a sign to the female, by raising the abdomen and bending it slightly sideways while walking up the reed stem." The female answers this signal "by moving the whitened end of her abdomen from side to side in a peculiar manner." After a dance-like flight together the couple mate with one



another. The method of pairing in Dragon-flies differs most strikingly from that prevalent among insects generally ; the tail processes of the male on the tenth abdominal segment do not clasp, as usual, the hinder region of the female's abdomen, but her neck. The actual copulatory apparatus of a male dragon-fly, exceedingly complex in structure, is situated toward the front end of the abdomen, on the second and third segments. To a central vesicle in this region the sperm-masses are transferred by the male flexing his abdomen ventrally so as to bring the opening of the ejaculatory duct on the ninth abdominal segment into contact with the cavity of the vesicle. Then, in the actual process of pairing, after the male has seized the female by her neck and prothorax, she flexes her abdomen strongly forward so that the spermathecal opening on her eighth abdominal segment is brought against his genital armature.

Dragon-flies, whose feelers are very small and poorly provided with sense-organs, appear to make little or no use of scent perceptions in their courtship and pairing. Among Lepidoptera, however, the sense of smell is often of great importance as a sex attraction, as has been mentioned in a previous chapter (p. 69), where reference was made to the "assembling" of male moths around a captive female ; moths thus attracted have usually complex feelers with sense-organs abundantly developed. The Swift Moths, whose recognition of mates through vision has just been described, have also the attraction of scent ; the male of *Hepialus humuli* emits from the bases of the hind-legs an odour that has been compared to that of almonds, and this probably acts as an auxiliary to his conspicuous white wings for an allurement to the female. In the smaller *H. hectus* both sexes are alike in their wing-colour ; the male's hind-legs are strongly swollen and the skin glands within these limbs secrete a fragrant fluid whose vapour carries a scent like that of the pine-apple. In these insects, therefore, the male is provided with attractive appearance or perfume or both ; but there is no definite evidence of choice being

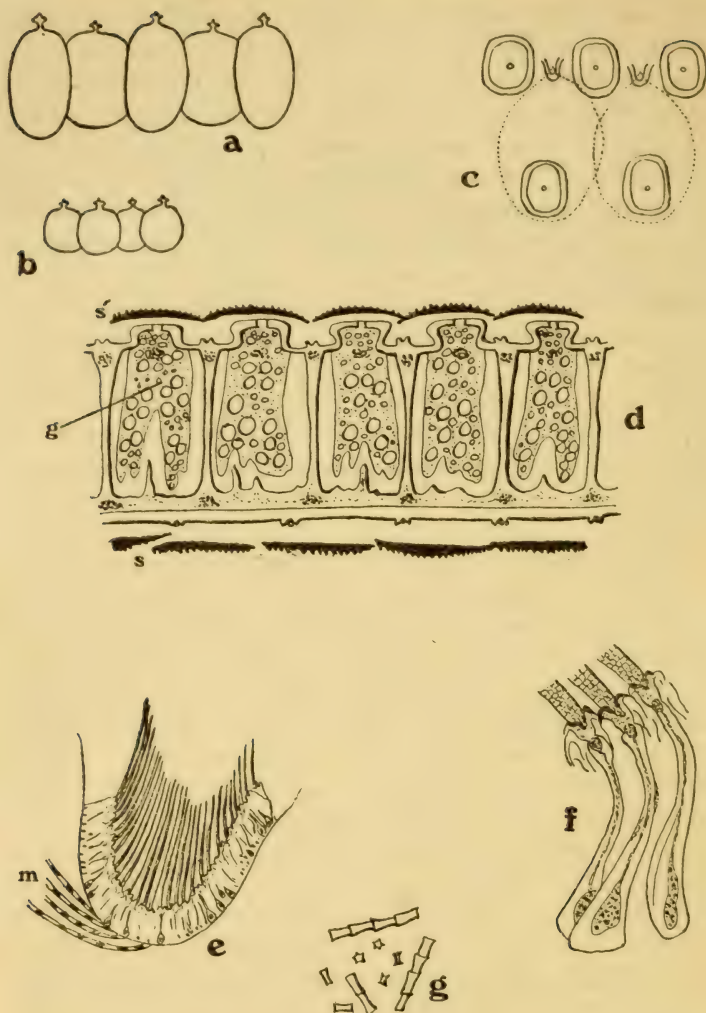


FIG. 56.—Scent-apparatus of male *Amauris niavius*. *a*, scales of general wing-area; *b*, scales of glandular patch,  $\times 160$ . *c*, scales (outline dotted) in relation to perforated chitinous projections,  $\times 350$ . *d*, section through wing showing upper (*s'*) and lower (*s*) scales and glands (*g*),  $\times 450$ . *e* section of abdominal "brush" showing filaments arising from cells, and retractor muscle (*m*),  $\times 100$ . *f*, cells of brush with bases of filaments,  $\times 200$ . *g*, fragments of filaments,  $\times 700$ . After H. Eltringham, *Trans. Ent. Soc.*, 1913.

exercised by the female for one special male among a number of others.

In many male butterflies of the Danaine group there are noticeable dull patches on the wings (either the fore or the hind pair) known as "brands"; these are clothed with scales, smaller than those clothing the general wing-area, and overlying little circular or ovoid "scent-cups" each covered by a cuticular lid with a minute central pore; beneath each of these is a multinucleate gland which secretes the odorous substance peculiar to the insect (Fig. 56, *c, d*). At the hinder end of the abdomen, in connection with the genital armature are paired "brushes" formed of elongate scales usually white or pale in colour. Each brush is carried in an extensible membranous bag; when this is everted by fluid pressure, the brushes appear as a conspicuous tuft at the male butterfly's tail-end. These remarkable structures on wings and abdomen have been well described by H. H. Freiling (1909) and by H. Eltringham (1913). The "brush-bag" in *Amauris niavius*, described by Eltringham, contains special groups of cells "which produce numerous delicate chitinous filaments, these having the property of breaking up transversely into innumerable tiny particles, thus forming a kind of dust" (Fig. 56, *e, f*). The butterfly, provided with this apparatus, brings the abdominal brushes into contact with the scent-brand on the wings, and then by everting them, scatters the perfume around, the "dust" apparently helping to diffuse the scent. The details of these structures vary in different members of the family. "Neither wing-glands nor dust-producing devices are invariably present; the brush itself and not the wing may produce the scent material . . . whilst the dust may be produced by the wing and not by the brush, and in the pupal instead of in the imaginal state." The scent emitted by these organs may be certainly regarded as an attraction to the opposite sex, but according to an observation made by Hale Carpenter (1920) its effect is not always immediately successful. A male *Amauris* in Uganda was "flying about after a female, which presently alighted on a dead flower-



spike. She . . . remained perfectly still while the male hovered a few inches above her head with a peculiar flutter causing him to rise and fall a little." The male displayed the "large, white brush-like structure . . . most energetically protruded and as rapidly withdrawn." But at length "the female suddenly flew away as if the performance had not appealed to her and the male followed." The reader of this unfinished story may imagine, if he please, that the courtship was finally successful.

Besides vision and scent, there is reason to believe that the females' power of hearing sounds produced by male insects of a few groups is an important factor in courtship. Reference has already been made (Chap. IV, pp. 80-82) to the stridulating organs on the legs and wings of male grasshoppers and crickets which produce the familiar chirping song of those insects, and the ears in the first abdominal segment or near the front knee-joint with which they are provided. It was also mentioned that some female crickets from which the ears had been removed were no longer attracted by the chirping of the males. Some positive observations on the value of chirping and hearing in the courtship of several species of European grasshoppers are due to E. B. Poulton (1896). Some of the males appeared to chirp in rivalry, and even to fight with each other by means of kicking or biting. The power of stridulation "seemed almost without exception to be exercised with direct reference to females, or in rivalry to other males in the presence of a female." In a species *Pezotettix pedestris* in which, the wings being underdeveloped in both sexes, stridulation is impossible, the male practises nothing that can be regarded as courtship, but jumps suddenly on a female and captures her as his mate. It is likely, even certain, that many insects produce sounds inaudible to us but appreciated by the auditory organs of their own species, and the perception of such excessively rapid vibrations may be of service in courtship. For example, the beautifully formed ear known as Johnson's organ in the base of the feeler of many male gnats and midges may enable these

insects to hear the high-pitched hum of the females and to direct their flight toward them.

Few insects display more remarkable habits in courtship than some predaceous two-winged flies of the family Empidæ, which have been studied by M. Howlett (1907) and A. H. Hamm (1908-9). *Empis borealis*, a fairly large species with russet brown wings, is common about mid-summer in our hill-districts, and a number of females may often be seen in "dancing" flight over the water of a stream. A male with an insect such as a stonefly or a mayfly captured as prey and carried in his legs, approaches, and after flying up and down beneath one of the females secures her and flies to some convenient plant-shoot. When observed there, it is seen that the prey has been transferred to the female by whom it is sucked during the process of pairing. "The male," writes Howlett, "usually hung by the front pair of legs to a twig, or blade of grass, supporting thus the whole weight of himself and partner; the middle legs clasped the thorax of the female, while the hind pair of feet supported the prey in position beneath her proboscis, the apical part of the femora meanwhile firmly compressing her upturned abdomen. The hind legs of the female hung idle while with the two front pairs she manipulated her prey, kneading it as one who sucks an orange dry, and every now and then turning it about to insert her beak in a fresh spot." The males were never observed to suck the prey which they caught nor did the females appear to catch any insects for themselves. Hamm describes the methods of capture practised by *Empis tessellata*: "the male sits in wait upon a leaf or grass stem, darting upon any fly coming near enough. If successful he immediately proceeds to hang by the tarsal claw of one of the anterior legs to the edge of a leaf or twig, the other five legs being tightly clasped round the struggling victim. He then proceeds to feel with the tip of the proboscis over the thorax of the fly, finally reaching and immediately piercing the junction between head and thorax. The proboscis was withdrawn after a few seconds, the victim being apparently paralysed

and only showing slight movements of the body or limbs. These observations seem to point to the conclusion that it is the central nervous system that is acted upon." Evidently these insects go through a complicated series of actions, the "dancing" movements of the females incite the males to catch prey and offer it to their desired mates, and the sucking of the victim's juices may stimulate the reproductive functions of the females.

The act of pairing is followed after a shorter or longer interval by that of egg-laying, in which we see the first, and in the case of many insects, the only manifestation of parental care. Some reference has already been made (pp. 75, 112) to the attraction of various female insects by chemical stimulus to substances suitable for the feeding of their young larvae or nymphs after hatching. A few further examples of the working of this function, extremely important for the life of the race, may be given.

The dragonflies, already mentioned in this chapter, afford an interesting diversity in the manner of their egg-laying. These insects live during their prolonged preparatory stages submerged in the water of ponds and streams, and the majority of females of the order drop their eggs "while flying over the surface of the water, merely by striking the tip of the abdomen from time to time against the water, and so washing off the steady flow of exuding egg-masses" (Tillyard, 1917). These masses of eggs are surrounded by a gelatinous substance, which may dissolve in the stream, "so that the eggs spread out on the river bed." In some cases, however, the effect of the water is to coagulate the gelatinous envelope which may then form a "rope," enclosing hundreds or thousands of eggs, twisted around the twigs of some aquatic plant. The females of the slender "damselflies" (Zygoptera), however, as well as those of the large, elongate Aeschnines, have two pairs of the processes of the ovipositor strongly developed as cutting organs with saw-like edges. By means of these, incisions are made in the stems of reeds or other aquatic plants, and the eggs



deposited therein singly or in small groups. The dragon-flies that provide such shelters produce egg-shells of the elongate form usual among insects, while the shells of eggs dropped into the water are rotund or shortly oval in shape. Some of the dragon-flies that cut incisions descend beneath the surface of the water in order to lay their eggs. It is remarkable that this provision of shelter in plant-tissue should be made, for the larvae when hatched are little beasts of prey, catching and feeding on weaker denizens of the water. In many dragon-flies the male continues his attendance on his mate throughout her egg-laying activities, so that both parents appear concerned in preparation for their offsprings' future.

In previous chapters reference has been made to the laying of eggs by female insects of various orders within or alongside some substance—plant-tissue, animal body, refuse, or carrion—that will serve as food suitable for the grubs after hatching. In many such activities the prospective mother in her egg-laying is reacting to an appropriate stimulation through her sense-organs of vision or smell, and it is perhaps dangerous to assign any psychic element to her behaviour. Yet her action tends definitely towards the provision of food for her young. Quite a number of insects, however, go beyond this indirect provision, and take trouble to collect food for their larvae before laying their eggs. The most striking examples of this practice are to be found among the Hymenoptera; the hunting and nest-provisioning habits of the digging-wasps have been mentioned in Chapter V (pp. 105-7), and some features in the activities of wasps, bees, and ants will be discussed in the next chapter on Social Life among Insects. For the present the food-providing habits of a common European dorbeetle (*Geotrupes typhaeus*), as described in one of the famous memoirs of J. H. Fabre (1907), may serve as an example of behaviour which cannot but suggest parental care. A male and female of *G. typhaeus* pair in the early spring and excavate a cylindrical tunnel running vertically down from the surface of the ground to a depth

of as much as five feet in some cases. The female does the digging with her strong fore-limbs, while the male hoists the displaced soil to the surface, a work in which the three sharp processes on his prothorax prove of much use by holding the fragments of earth. He then collects sheep-dung, which in the upper part of the tunnel he works into pellets with his thoracic spines and front legs, breaks into large fragments, and lets fall to the lower part of the tunnel where the female reduces these fragments to a fine state of division and arranges them in the form of a "sausage" or "long cylindrical loaf." The egg is laid a short distance below the food-mass, to reach which the grub after hatching "will have to demolish and pass through a ceiling of sand some millimetres thick."

From such provision of food-supply by father and mother for their young, we may pass to actual care for the family after hatching as well as for the eggs. This is illustrated by the habits of our Common Earwig (*Forficula auricularia*) and other members of the same lowly family. More than a century and a half ago C. De Geer (1773) observed the female of the Common Earwig brooding over her eggs, and M. T. Goe (1925) has lately stated that the eggs will not hatch unless this incubation has been practised. The incubation period lasts for about a fortnight, and after hatching, the young earwigs are often tended for some time by their apparently careful mother. A pleasing sight is presented to the naturalist, lifting a partly sunken stone beside a hedgerow in winter or spring, by a female earwig with her eggs or her tiny pale youngsters, already strikingly like her in general aspect, but with the forceps-limbs relatively slender and weak. The larger shore-hunting earwig *Anisolabis maritima* has, according to C. B. Bennett (1904), similar breeding habits. The female, in preparation for egg-laying, hollows out beneath a log or stone, a "little chamber" an inch wide and half as deep, carrying away the excavated soil between her jaws. "The chamber is made perfectly clean; no sticks or bits of wood or pebbles are allowed by the more careful females to remain." The eggs

themselves, after being laid are carefully rolled and cleaned in the mother's mouth ; then they are watched and guarded until hatched, as are the young also for at least a few days. The female *Anisolabis* does not, however, maintain for long her reputation as a good mother, for when the family " had once left her to seek food for themselves they could not safely return lest she should endeavour to eat them."

Similar but more prolonged care for offspring is shown by a common European and British Shield-bug *Acanthosoma griseum*, whose habits were, like those of the earwig, observed in the eighteenth century by De Geer. His observations have been confirmed by several naturalists whose notes are conveniently summarised in the recent work of E. A. Butler (1923). E. Parfitt watched how the mother shield-bug " came to the rescue " of a youngster touched by him with a twig, " putting her antennae down to the little thing and drawing them over it." J. Hellins saw a family of twenty newly-hatched young bugs beneath a birch-leaf covered, together with the empty egg-shells, by their mother's body. At a later stage of their development he writes that she " was now quite in a state of fuss . . . if I attempted to touch her brood she fluttered her wings rapidly . . . at night when the wind blew roughly, the mother contrived to get them under her, and sat covering them as at first." The point at which the story ends suggests the progress of many other families ; the young were seen " just setting off on their travels," then " busy exploring," while " the mother ran from place to place feeling for them." There is also some evidence for maternal

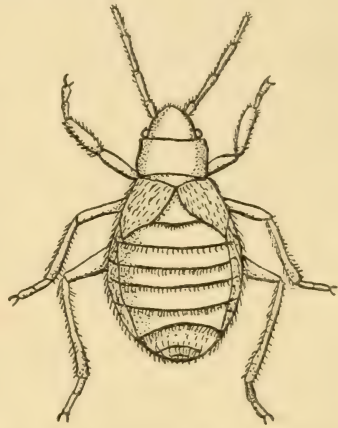


FIG. 57.—Seashore Bug (*Aepophilus bonnairei*) coasts of South Britain, Ireland and W. Europe.  $\times 10$ .



care in the small bug *Aepophilus bonnairei* (Fig. 57) which lives on the sea-shore between tide-marks. A number of young beneath a stone, kept for observation by J. H. Keys, arranged themselves in a circle facing the mother in the centre. When the stone was lifted, "the adult would almost instantly alarm the young with a rapid tap with each antenna alternately, and the whole troop would scamper round to the other side of the stone with great speed."

Undoubtedly one of the most remarkable of all recorded cases of family life among "non-social" insects is that of the European horned dung-beetles (*Copris*) whose habits are described in a well-known memoir of J. H. Fabre (1897). These insects do not roll balls of dung about as their allies the "sacred" beetles (*Scarabaeus*) do. For their own food-supply they excavate beneath lumps of excrement lying on the surface of the land, and "here is engulfed without definite shape, an enormous supply of victuals, bearing eloquent witness to the insect's gluttony." In the breeding season, which comes in May or June, however, a pair of *Copris* work together, digging out a spacious ovoid chamber, within which sheep-dung, collected by the male, is comminuted and kneaded by the female into an egg-shaped mass. This is later subdivided into several pellets on each of which the female carefully forms a shallow basin-like cavity, lays an egg therein, and covers it by judiciously applied pressure. The male of *Copris hispanus* leaves all this work to his mate, but in *C. lunatus* the father remains underground and as a result of his assistance the pellets are twice as numerous as in the other species. In the former case the mother, in the latter both the parents, keep guard for several weeks over these pellets within which the grubs are developing. In due time the larvae pupate, and at length the young beetles are perfected and emerge; they make their way to the surface of the ground accompanied by their parents, who thus have the privilege—very rare among insects outside the "social" groups—of seeing the members of their family reach the adult state. It is this unusual condition which makes

Copris of especial interest to the student of insect biology from the comparative point of view. It is believed that all through the weeks during which the young are developing the parent keeps guard, fasting in the underground chamber—her behaviour contrasting markedly with the “gluttony” in which she indulged before the breeding season.

Nearly related to the Scarabs and their allies are the Passalidae—a group of large flattened beetles, black or brown in colour, distributed through the tropics and warmer regions of both hemispheres. These also display a family life of quite remarkable interest, which has been elucidated by F. Ohaus (1899–1900) and W. M. Wheeler (1923). They live in galleries eaten out in decaying timber. The parents guard the eggs after laying, and prepare food for the larvae after hatching by breaking up the wood with their jaws and partly digesting it. This is necessary because the grub's jaws are too weak for direct attack on timber; the larvae “are therefore compelled to follow along after their tunnelling parents and pick up the prepared food.” In the darkness of their burrows, the Passalid beetles and their grubs communicate with each other by audible signals, the beetles stridulate by rubbing toothed surfaces below the wings over similar surfaces on the abdomen, while the grubs scrape the strong denticles carried by their very short, unjointed “paw-like” hind legs over striated areas on the sides of the thorax. The care of the parent Passalids is said to be continued through the pupal stage of the offspring until they assume the condition of mature beetles.

The order of the Hymenoptera is well known as exhibiting the most striking examples of parental care among insects. In a previous chapter (V) some account was given, in connection with a discussion on insect behaviour, of the egg-laying, nest-making, and provisioning habits of various digging wasps. Such creatures provide beforehand for the needs of their offspring, but the mother does not survive to see the hatching of the grubs and tend them as a family. Many female Hymenoptera, however, have this relationship with their young, and examples are afforded by the

comparatively lowly family of the Sawflies (Tenthredinidae) whose larvae are caterpillars (Fig. 76, *b*) feeding on leaves. The habits of Australian species of *Perga* have been described by R. H. Lewis (1836) and W. W. Froggatt (1891, 1918). The female *Perga lewisii* lays about eighty eggs in an incision cut between the two surfaces of a gum-tree leaf, and rests on the leaf until the eggs are hatched ; after this she follows the young caterpillars about as they feed, " sitting with outstretched legs over her brood, preserving them from the heat of the sun, and protecting them from the attacks of parasites and other enemies." When fully grown the larvae crawl down to the ground-level and spin cocoons for pupation in the soil. In the later stages of larval growth, these caterpillars are no longer guarded by their mother, but they continue to feed and move in companies so that they may still be regarded as a family living to some extent at least a common life. Such gregarious habits, often resulting from the limited space available on the food-plant, are displayed by many sawfly caterpillars, as well as by caterpillars of moths and butterflies (Lepidoptera). The local migrations of swarms of larvae of the Antler Moth (*Chareas graminis*) or the Vapourer (*Orgyia antiqua*) are impressive. Members of such communities move together, apparently guided by contact, their behaviour suggesting that they should be regarded less as a family than as a flock. The family association among untended larval insects seems most apparent in cases where the young creatures by their united labour spin a silken web over the twigs and leaves of their food-plants, and live together on this shelter, a kind of nest not provided by the parent but made by members of the family. The caterpillars of the Peacock Butterfly (*Vanessa io*) afford illustrations of this habit in their younger stages, while the caterpillars of the Lackey Moth (*Clisiocampa neustria*) and the Small Ermines (various species of Hyponomeuta) practise it throughout larval life. The silken cobweb-like habitations of numerous families of the last-named group are often so close together that the plants on which they feed, a hawthorn hedge, for example, appear



covered by a continuous sheet of fine threads, and the families of caterpillars are merged in a great, if unorganised, society.

Returning to the Hymenoptera that store in their nests provision for their grubs by burying or immuring paralysed or dead caterpillars and other prey, it is of interest to find traces of the development from this common habit to that of actual care for the grubs after hatching. In his most instructive work on "Social Life among Insects," W. M. Wheeler (1923) draws attention to the habits of certain African solitary wasps (*Synagris*) as described by E. Roubaud (1916) and J. A. Bequaert (1918). These wasps make mud-nests on such surfaces as the thatch of huts, and the female "under normal conditions, when food is abundant, lays an egg in her mud cell, fills it in the course of a few days with small paralysed caterpillars, and then closes it." But when prey is scarce the mother-wasp guards the egg, and after it hatches, collects a few caterpillars at intervals so as to provide food for the grub during the greater part of its period of growth. When the larva is about three-quarters grown, the mother "immures it in its cell with the last supply of provisions." In such species therefore we see actual transition from the storing of food for grubs which the mother will never see to actual care and feeding of the young. This has apparently become the normal habit of one species, *Synagris cornuta*, as the female feeds her offspring "from day to day with pellets made up of a paste of ground-up caterpillars." The habit of bringing food to the larvae through their period of growth is well known in the Sphecoid digging-wasps of the genus *Bembex*. The habits of the North American *B. spinolae* have been vividly described by the Peckhams, who dwell on the female's "habit of feeding her young from day to day or rather from hour to hour as long as it remains in the larval state." These insects catch two-winged flies which are placed in the nest after having been killed by stinging. Wheeler remarks how the number or size of the victims is increased "as they are needed by the growing and increasingly voracious larva."

Like the wasps the great majority of bees provide for their young by storing food—honey and pollen—in the nests wherein they lay their eggs, the nests being made in tunnels excavated in the soil, by species of *Andrena*, *Colletes*, and *Megachile* for example, or in the twigs of plants as by the well-known *Osmiae*, or in dry wood as by the “carpenter” bees (*Xylocopa*), or in remarkably firm structures of stone-fragments and cement as by the “mason” bees (*Chalicodoma*). Among all these the nest-chamber is sealed up with the egg and the store of food, and the mother bee never sees her offspring. The habits of *Osmia tridentata*, as described by J. H. Fabre (1891), afford an example of what may be regarded as family relationship. The female of this species lays eggs in a series of chambers along a hollow bramble-stem, each chamber with a provision of food for the grub after hatching, and the grub when fully grown spins a cocoon and pupates. When a young bee emerges from the pupal coat, it bites its way through the cocoon, and then through the partition closing the chamber in which it has been reared. Should the young insect be in the last-formed chamber next the opening of the hollow twig, it comes out at once into the open and begins its active aerial life. If, however, it finds the way to liberty blocked by the cocoon of a younger sister it waits for her emergence or tries to press a way between her cocoon and the wall of the chamber; it is stated that a young *Osmia* never injures other members of the family in attempts to escape from its nest. Although the last-laid egg is nearest to the outlet and the first-laid in the nest farthest from it, the young do not necessarily complete their development in the regular order that might be expected; the older offspring may have to wait comparatively long for the emergence of their younger sisters, or these latter may complete their transformations more rapidly than those hatched from the earlier laid eggs and so get out of the way in good time.

It is of interest to note that the perfect insects among the Hymenoptera commonly take food of the same kind as they provide for their larvae. Bees as well as bee-grubs

feed on honey and pollen. Wheeler has pointed out how an ichneumon fly sometimes licks up the blood of insects that she has pierced with her ovipositor, and that this organ may thus be used for self-feeding as well as for reproduction. Somewhat similarly a digging-wasp, seizing a caterpillar between her mandibles, may bite the neck of the victim, and take a portion of liquid food from it for herself, before depositing it in her nest as a food-store for her offspring. This possibly close association of the feeding with the reproductive instincts is believed by Wheeler to have been of great importance in the development of true social life among insects from such ordinary family relationships as have been considered. Some of the wonderful and fascinating facts and problems of insect societies may now therefore demand our attention.



## CHAPTER IX

### SOCIAL LIFE

THE social life of insects may be fairly regarded as the central subject in our presentation of the biological study of these fascinating creatures, since the habits of such societies as those of the bees and ants are commonly known in their main features, and have attracted during many centuries the admiring notice of mankind. A community of bees, ants, wasps, or termites is a family, of which the individual members are greatly multiplied and their association for common activity so highly organised that the individuality of the single insect becomes merged in the wider individuality of the complex, social organism. Such insect societies as these are by far the best known, but there are others in which the community consists not of one huge family, all the offspring of a single abnormally fertile mother, but of an assemblage of families living together in such a way as to promote mutual protection and provision. W. M. Wheeler, whose comprehensive treatise (1923) on the social insects has been already referred to, enumerates as many as twenty-four different groups of insects among which a common way of life has become more or less completely adopted. It is, however, doubtful if all of these can be regarded as having developed so far beyond the simple family relation as to attain a truly social state. Wheeler himself designates fourteen of his twenty-four groups as "incipiently social or subsocial." It hardly needs to be stated that very many insects, locusts, dragonflies, butterflies, midges, for example, which are occasionally or habitually gathered into flocks, cannot be reckoned even

among the "sub-social" groups; the members of such a flock keep near their companions, but in their activities they show no such mutual co-operation as characterises a true insect community.

Examples of insects which live in societies made up of an assemblage of many families are afforded by several groups of beetles. The family life of the Passalidae was described in the last chapter (p. 213), and the conditions of their existence—parents and offspring feeding in galleries excavated in timber—afford a starting-point for the more distinctly social habits of the "ambrosia" beetles, which are akin to the destructive "bark-beetles" of our forests. Most of these Scolytidae (or Ipidae) eat bark or wood, both in their larval and adult stages, but the "ambrosia" beetles have developed a more elaborate method of feeding and a simple type of social life. The habits of various European and North American species of *Gnathotrichus*, *Xyleborus* and *Platypus* have been described by H. G. Hubbard (1897) and others whose accounts are summarised by Wheeler (1923). While most of the Scolytidae make galleries at the inner surface of the bark, the ambrosia beetles burrow deeply into the wood; it is not wood, however, on which they feed, but a fungus—the "ambrosia"—specially cultivated on a "bed" prepared from woody material which has passed undigested through the insects' food canals. Beetles of both sexes work together, but most of the parental care devolves on the mother, who excavates a series of circular pits along the tunnel, laying an egg in each and depositing fragments from the "bed" with some growing fungus as food for the grubs when hatched. Each grub as it grows increases the size of its "cradle" (Fig. 58, G', I) by biting and swallowing wood which is not digested but, being ejected in pellets from the intestine, is removed by the mother and used for fungus-bed. "The mouth of each cradle is closed with a plug of the food fungus, and as fast as this is consumed it is renewed with fresh material." The females of *Platypus* lay eggs in groups of ten or twelve at intervals along the

galleries, and the grubs when hatched "wander about in the passages (Fig. 58, P) and feed in company upon the ambrosia which grows here and there upon the walls." Probably each kind of ambrosia beetle "grows its own peculiar fungus in a pure culture," and each female starts a new culture for her offspring by carrying away from the cradle or passage in which she was herself reared a mass of

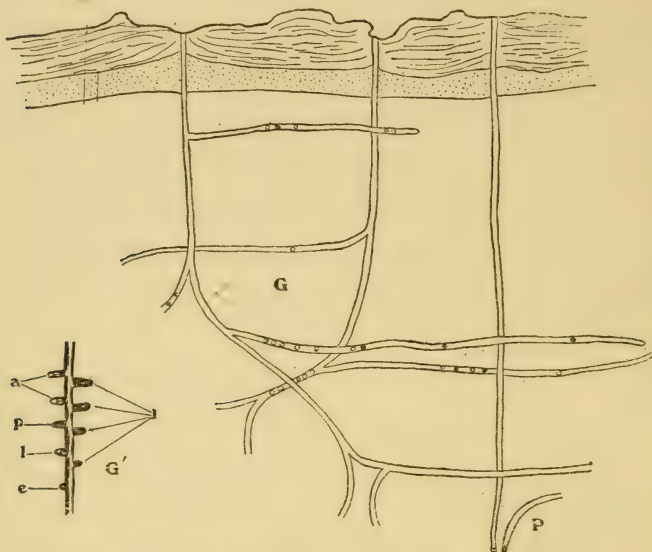


FIG. 58.—Galleries of Ambrosia Beetles. *Platypus* (P) and *Gnathotrichus* (G) in pine trunk. North America. The small circles along the course of the galleries, as seen in cross section of trunk, indicate position of the "cradles," which are shown in side-view at G' (e, egg; l, larvae in various stages; p, pupa; a, adults waiting for emergence). About natural size. After J. M. Swaine. (*Canad. Dept. Agric. Ent. Bull.* 7, 1914.)

spores, either on her head, in her jaws, or in the front region of her stomach, whence they are regurgitated when she has reached a site suitable for the foundation of a new family.

Most remarkable perhaps of all the social beetles are two forms of the family Cucujidae recently found by Wheeler living in the hollow leaf-stalks of young *Tachigalia* trees of



the Guiana forests. These are small, narrowly elongate insects with clubbed feelers and short legs, which, after entering the hollow stalks, live and feed along strands of especially nutritive tissue; after a time their excrement accumulates in longitudinal ridges adjacent to the "food-grooves." Following the beetles, large numbers of small mealy bugs (*Pseudococcus*) invade the hollow stalks and begin also to feed along the nutrient strands; then the beetles and also their larvae go to these mealy-bugs for nourishment, stroking with their feelers the little white sucking insects and inciting them to discharge from their intestines the sweet honey-dew. When two or more beetles," writes Wheeler, "or two or more larvae or a group of beetles and larvae happen to be engaged in stroking the same mealy-bug, they stand around it like so many pigs around a trough, and the larger or stronger individual keeps butting the others away with its head." From this account it seems that the "self-regarding" instincts are not wholly eliminated in the social life of these beetles of the *Tachigalia* trees. Wheeler, in his account of these insects, lays stress on the fact that they are found in the leaf-stalks only so long as the trees are young enough to form part of the forest undergrowth. "The older trees . . . have all their petioles inhabited by viciously biting or stinging ants." These latter invade the leaf-stalks as the tree grows, driving out the beetles, but preserving the mealy-bugs and adapting these "cattle" to their own use. It is well known that many societies of insects, and especially ants, harbour a miscellaneous assemblage of "guests," some of which are clearly of service to their "hosts." It is of much interest to trace in the succession of insect inhabitants of the leaf-stalks of these tropical American trees the varying relations between the plants, the mealy-bugs, and the two strikingly diverse types of communities, first beetles and then ants, which successively make use of other organisms for obtaining shelter and food.

We may now pass on to consider the social life of those

well-known groups of Hymenoptera, the wasps, bees, and ants. As previously mentioned, the societies of these insects are in reality large, often immense, families, and the family life of some wasps and bees has been described in the preceding chapter. In a typical insect community belonging to one of these groups, the vast majority of the population are those modified females, known as "workers," usually infertile and often in some way specialised for carrying on the essential activities of the society. The fertile females in a nest, actual or potential mothers, are known as "queens." Among the greater number of genera of wasps and bees, such as those mentioned in the last chapter, the individual insects are all normal, fertile females and males. There are no workers, and these insects are commonly termed "solitary"—a term that may be considered not altogether appropriate, for though the family does not grow into a great society, a number of females of the same kind often make their nests close together, as with *Synagris* among the wasps and *Andrena* among the bees; but although scores or hundreds of such wasps and bees have their nests close together there is no co-operation between the different mothers or their families.

The hymenopterous society being a very large and more or less specialised family, we expect to find some indication of its mode of development from an ordinary family, and Wheeler suggests that the habits of certain wasps indicate stages of transition between the "solitary" and "social" way of life. F. X. Williams (1919) has shown how some species of the eastern tropical *Stenogaster* are solitary while others approach the social habit, as they construct nests of several chambers, sometimes enclosed in an envelope, the mother feeding a number of larvae at the same time, sealing up the chambers when they are fully fed, and sharing the nest with her daughters when these have attained the adult condition. None of the *Stenogaster* females, however, appear to be infertile or to be in any way specially modified as workers; the adult inhabitants of the nest are relatively few in number, and it is doubtful how far the daughter-

wasps help the mother in feeding the younger grubs. The societies of the African *Belonogaster* (Fig. 59) are larger, but again all the daughters of a family community are fertile, and parties of them, at intervals, leave the parent nest together to found fresh societies, each of which consequently possesses as many potential mothers as there are foundresses.

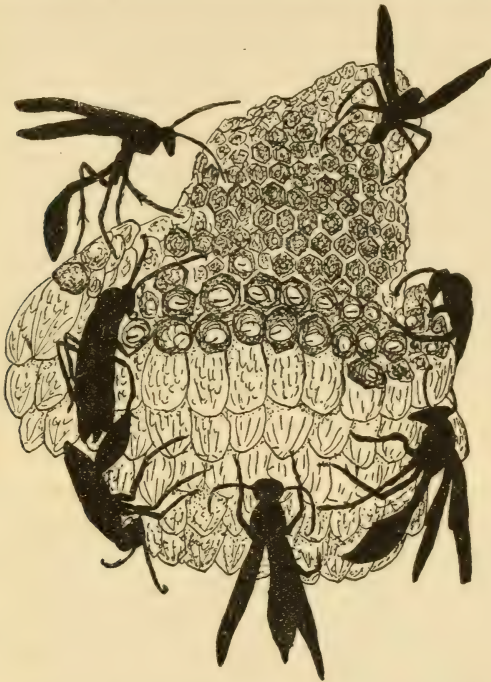


FIG. 59.—Nest of Wasp (*Belonogaster junceus*), West Africa. Above chambers with eggs, lower with larvae, at bottom closed cocoons. Adult wasps, males and females, the latter attending and feeding the larvae, both obtaining the larval salivary secretion. Drawn from a photograph, E. Roubaud (*Ann. Sci. Nat. Zool.* (10) i. 1916).

In allied South American wasps occurs a differentiation between the normal fertile females or queens and the smaller females (workers), with reduced or vestigial ovaries which if capable of producing eggs, lay only unfertilised ones which may all be expected (see p. 140) to develop into males. These American insects “regularly form new



colonies and nests by sending off swarms of workers with one or two dozen queens." The plurality of mothers ("polygynous" condition) results in their nests becoming crowded with "hundreds or even thousands of individuals."

Most of the tropical social wasps are similarly polygynous, whereas the widespread *Vespa* (represented by seven species in Great Britain) has only a single queen-foundress for each nest. After surviving the winter she starts a new family and habitation in the spring. Of course, a proportion of the young female insects reared in one of our native wasps' nests develop into queens, but the vast majority are workers. It is of great interest to find that females of an intermediate type may occur, smaller than a queen, larger than a worker, and with ovaries reduced yet functional. O. H. Latter (1904) points out that these "fertile workers" are developed as the effect of an especially rich food-supply being available for the grubs in certain seasons. The workers of *Vespa* feed the grubs on fragments of captured insects, bitten up, malaxated by moistening with saliva, and moulded into small pellets. The wasp larvae in the chambers of the comb thrust out their heads, as Wheeler remarks, "like so many nestling birds, and when very hungry may actually scratch on the walls of the cells to attract the attention of their nurses." It is now, however, well established that the feeding activities in a wasps' nest are by no means one-sided. P. Marchal (1896), C. Janet (1903), E. Roubaud (1916), and other observers have found that the parent or nurse-wasps obtain from the larvae which they tend sweet saliva often in large quantity, and Wheeler (1923) supports the opinion that this drain on the larval food supply is a potent physiological factor in preventing the development of the young insect's reproductive system, so that it becomes a sterile worker instead of a queen. Wasps in a nest engaged in tendance of the grubs stimulate the mouths of these by contact, or even by seizure of their heads between their own mandibles in order to incite the secretion and flow of the desired fluid. In some cases at least it has been estimated "that there is a flagrant disproportion between the quantity of nourishment

PLATE VIII



NEST OF TREE-WASP (*Vespa norvegica*). One-tenth size.



NEST OF GROUND-WASP (*V. germanica*), dug out by a Badger. One-tenth size.  
[To face p. 224.]

[H. Britten, photo.]





distributed among the larvae by the females and that of the salivary liquid which they receive in return." This comparison is made by Roubaud, who does not hesitate to accuse the nurses of "actual exploitation of the larvae." The males or "drones" in the nest though they bring no food to the grubs take from them the sweet fluid (see Fig. 59). Roubaud and Wheeler believe that the evolution of the family society is to a great extent a result of the reciprocal feeding ("trophallaxis"); there "naturally follows a tendency to increase the number of larvae to be reared simultaneously in order at the same time to satisfy the urgency of oviposition and to profit by the greater abundance of the secretion of the larvae."

The bees, which must now be considered, have, it is calculated, only about 500 out of their 10,000 species living in true social communities whereof specialised worker-females form the great majority of members. The wasps are predominantly predaceous, though many of them feed on vegetable substances occasionally or habitually. The bees, however, are as a group dependent on the products of flowers—on the nectar which after digestion in the insects' stomachs becomes honey, and on pollen; the broad shin and basal foot-segment and the feathered hairs of bees, among the most striking of their structural features, are connected with the habit of gathering pollen from the floral anthers, while the tip of the labium is elongated to form a beautifully efficient organ for licking up fluid from the nectaries of blossoms. "Solitary" bees, among which no workers occur, provision their nests, as we have seen, with honey and pollen, usually mixed to form "bee-bread," partitioning the nest into chambers each of which contains at first an egg, later a grub with its appropriate store of food. In certain species of *Halictus*, which nest in burrows in the ground, the mother closes up the chambers, but guards the nest afterwards and survives till the development of the young is complete; there is, however, not time enough for the realisation of social life between her and her offspring. Wheeler quotes some very interesting recent

observations made by H. Brauns on South African species of *Allodape* which nest, like our native *Osmia*, in hollow plant stems, but make no partitions between the successively laid eggs so that the nest is not divided into chambers. In some species a "food-packet" is provided for each grub at the time of egg-laying. In others the mother arranges the eggs in such a way that the grubs, when hatched, direct their heads towards the entrance of the nest, and she brings to them at intervals lumps of "bee-bread" on which they feed in common. A further stage of development in behaviour is attained by species of *Allodape* whose females feed their grubs individually, and produce an "affiliation of the offspring with the mother to form a co-operative family." No workers, however, are produced among these incipiently social bees, and it must be admitted that the three truly social groups—the bumble-bees, the stingless bees, and the Hive-bee with its wild allies—stand markedly distinct from all the rest of the family. A feature of structure in relation to life conditions that characterises them is the possession of abdominal glands that secrete the well-known bees-wax used by the insects for building the chambers of their combs.

The stoutly built hairy bumble-bees (*Bombus* and allies) are well known to every country rambler, and the habits of our British species have been excellently described by F. W. L. Sladen (1912). The societies of these insects in temperate climates are in most respects parallel to those of the social wasps, in that a queen, reared and paired in the previous summer, survives the winter in some sheltered spot and starts a new family in the spring. The young queen chooses in autumn a bank with a northern aspect on which to seek a burrow for hibernation; on a south-facing slope she might be awakened by the midday sun too early in the year and perish in a sudden frost. For the site of her nest (Plate IX) she seeks some convenient underground cavity, often the deserted burrow of a field-mouse, and begins her building work by moulding a lump of moistened pollen on which she erects a waxen wall enclosing

PLATE IX



NEST OF BUMBLE-BEE (*Bombus muscorum*).

*To face p. 226.*]

[*J. W. Dixon, photo.*





a cup-shaped hollow where the first eggs may be laid ; she constructs also a small round-mouthed, waxen honey-pot. She broods over the eggs to incubate them and covers them with a thin layer of wax. The young grubs "devour the pollen which forms their bed, and also fresh pollen which is added to the lump by the queen," who also feeds her offspring with a mixture of pollen and honey which is squirted into the larval chamber through a small hole bitten by the queen in the waxen covering. While the larvae remain small they are fed collectively, but "when they grow large each one receives a separate ingestion." The chamber within which they are developing increases in size, and when, less than a fortnight after hatching, they are fully grown, each spins round itself a thin, tough, paper-like cocoon and pupates. All the early bees of the family are small infertile females or workers, which when they become active, take on the work of nest-making and grub-tending, while the queen confines her attention to laying eggs. As with the wasp communities, the population of a bumble-bee nest grows through the summer, though it rarely exceeds a final total of a few hundreds. The undeveloped condition of the workers may be explained as due to poverty of feeding ; later in the season, when the total number of larvae in a nest becomes diminished, young queens are reared, as well as males, the latter arising (see p. 140) from unfertilised eggs. As with the wasps again, neither workers nor males survive the winter ; only the young queens hibernate so as to renew the race in the succeeding spring. In tropical regions, however, the bumble-bee community survives through a number of years, and over-population is relieved by means of a succession of swarms.

The Stingless Bees (*Meliponinae*) are a small group confined to tropical countries and most abundant by far in South America. They are of small size and the stings of the females are so far reduced as to be useless as weapons. They are structurally more specialised than bumble-bees, as the queens have narrow shins and proximal foot-segments

—a degenerative modification—while the workers except for their sterility represent “the typical female of the species.” Wax “is produced by the males as well as by the workers—the one case in which a male Hymenopteran seems to perform a useful social function,” as Wheeler remarks. In the communities of stingless bees the activities of the nest are carried on by the workers, the queen’s functions being from the beginning confined to reproduction ; hence for the foundation of a new community a swarm comprising a queen with some workers is essential. These insects construct nests usually with layers of waxen comb consisting of hexagonal chambers with the openings on top. Their habits are curiously primitive, for the workers, according to Wheeler’s account, “put a quantity of honey and pollen into each cell, and after the queen has laid an egg in it, provide it with a waxen cover, so that the larva is reared exactly like that of a solitary bee.” But they have the habit of storing food in special receptacles ; H. W. Bates (1863) described the nest of a Brazilian *Melipona* which contained “about two quarts of pleasantly-tasted liquid honey.”

The Hive-bee group (*Apis*) are the most highly specialised of the family, and the exceedingly ancient domestication of the common species by mankind has rendered it one of the most familiar of all insects. Some aspects of the association of bees with our own race will be discussed later in this volume (Chap. XIV) ; for the present it is sufficient to suggest that the conditions under which domestic bees are reared, in straw skep or wooden hive, are modified from the manner of life of their wild ancestors. The few wild species of *Apis* all inhabit south-eastern Asia. *Apis dorsata* and *A. florea* build typical waxen combs in a single layer with two series of chambers arranged back to back and opening horizontally, suspended openly from the branches of trees. *A. indica* (hardly separable as a species from the domestic *A. mellifica*) makes a number of similar combs hanging side by side in hollow trees, and this is the habit of communities of *A. mellifica*



which, escaping from the tutelage of mankind, have become feral, reverting to an independent mode of life. Sometimes, however, feral nests of the hive-bee are found hanging without protective covering from the branches of trees. All these facts combine to indicate that the genus *Apis* originated in the tropics of the Eastern Hemisphere, and that it has become adapted to life in cooler regions by the habit of nesting in shelters either discovered or provided.

In their mode of life, shown among the truly wild as well as in the domesticated species, the hive-bee group is distinguished by a marked "division of labour" between workers and queen and by the progressive feeding and tendance of the larvae throughout life. Details of the economy of hive-bees have been frequently described, and no more need here be attempted beyond the indication of a few leading facts of especial biological interest. These insects store honey in some of the chambers of their comb, and thus ensure a constant and convenient supply for the growing grubs as well as for the adult bees in the nest. The habit renders possible also the persistence of the community from year to year in those northern countries with cold winters where hive-bees have been for centuries domesticated. New communities are established by swarms, consisting of a queen with a crowd of workers, which leave the old habitation. Swarming in the domestic bee-communities follows the emergence of a daughter-queen—an event controlled by the workers. The daughter remains in the hive, and the swarm is "led off" by the mother-bee.

The worker bees take over all the activities necessary for the rearing of the young: comb-building, food-gathering, and distribution, and they also control by collective action the reproductive function of the queen, who may be regarded as "a mere egg-laying machine entirely dependent on her worker-progeny." Her hind legs are destitute of those pollen-gathering adaptations so elaborately developed in the workers, though among the bumble-bees these are common to queens and workers. As an egg-laying machine, however, the queen-bee is highly efficient, as she may produce

1,500,000 eggs during her life. As mentioned previously (Chap. VI), female Hymenoptera are developed normally from fertilised and males from unfertilised eggs, and it is well established that the growth of a bee-grub hatched from a fertilised egg either into a queen or into a worker depends on the nature of its food. Larvae destined to become queens are reared in large ovoid "queen-cells" situated at the edge of the comb, and fed throughout their growth with "royal jelly," believed to be a secretion of the worker's pharyngeal glands. Worker-grubs, on the other hand, receive this food only for the first four days of their development after hatching; during the final two days of larval life they are fed by the workers on honey and pollen. The food of the queen-larvae is relatively very rich in fat, that of the worker-larvae in sugar. That the kind of female developed from a fertilised egg is determined by feeding has been often proved experimentally by transferring very young grubs from one kind of chamber to the other. The male bees are developed from unfertilised eggs which the queen lays in "drone-cells" of hexagonal shape like the worker-cells but of larger size; when laying these the queen-bee releases no spermatozoa from her sperm reservoir, as she does when laying in cells provided for the rearing of female bees. This is doubtless the general mode of procedure, but reasons have already been given (p. 140) for allowing the possibility of the exceptional origin of male bees from fertilised and of females from unfertilised eggs.

Besides the "brood-comb" in which the grubs are reared many series of chambers form a "honeycomb" for the storage of food. It is from this store that the grubs are supplied, and it has long been known that the first period of a worker-bee's life after emergence from the pupal coat, is spent within the hive, and that expeditions for the gathering of nectar and pollen are not undertaken until she has attained a certain age. It has been recently stated by G. Roesch and K. von Frisch (1925) that there is a routine of duties through which all the workers of a hive successively pass. The first work of a newly emerged bee is to

clean out chambers of the comb ready for egg-laying ; her next to remain in chambers where eggs have been laid, apparently for the purpose of assisting incubation. During the early period she is fed by her sisters, but when about three days old she begins to collect pollen and honey from the store, some of which she uses herself, but passes on most to the older grubs. When about a week old, her own digestive system becomes fully active and she spends the next week in feeding the young grubs that require her secretions for their proper nourishment. Then she begins to take up a certain amount of outdoor work, trying her powers in exploring flights, receiving nectar and pollen from the older foraging bees and removing dead comrades and refuse from the hive. The foraging bees on returning to the nest " dance " on the honeycomb with a circular turning motion, and during this performance the younger workers surround them with the apparent object of appreciating and remembering the scent of the flowers which the foragers have been visiting, so that these younger members when they in their turn leave the hive on foraging flights are guided to the same sources of food supply in special kinds of flower. The rapid, changing activities of a worker-bee at the height of the honey-season soon wear out the insect's constitution, and her life may last no longer than three weeks. Worker-bees, unlike the wasps, derive no food-substance from the grubs that they tend. The habit of storing a large reserve of honey and pollen in the nest ensures an abundant supply for adult insects as well as grubs, so that there is no exploitation of the latter by their nurses. The life of the worker-bee is devoted to the service of the society whereof she is a member, and her varied activities, briefly sketched in these pages, which follow one another in regular order as responses to successive stimulations, indicate to how great an extent her behaviour is regulated by inherited instinct. Our wonder at the matter is increased as we recollect that neither the remarkable structures on which her activities depend nor the instincts themselves are characteristic of the parents, queen and



drone, through which the inherited characters are transmitted.

Most insect communities harbour a number of other insects which live during a part or the whole of their lives as "messmates," "guests," or parasites. The large population of a wasps' nest or a bee-hive may contribute to render such association easy and profitable to the invaders if not to the "hosts." It is possible only to refer to some of these invaders that are definitely related to the social life of the host-insects. The large two-winged (Syrphid) flies of the genus *Volucella* are conspicuous British insects, whose curiously formed maggots, provided with elongate processes on the body segments, live, in the case of *Volucella inanis* in the nests of social wasps, and in the case of *V. bombylans* in those of bumble-bees. The former fly has a yellow-banded abdomen like a wasp, and the latter is hairy like a bumble-bee. Both enter freely into the nests of their respective hosts in order to lay their eggs, and the maggots, after hatching, live on the combs, where they appear to act as scavengers by devouring refuse, thus performing a definite service to the community. There is no evidence in support of statements that have been made to the effect that the *Volucella* maggots devour the grubs of the wasps and bees; the position in the nest where the syrphid larvae live indicates that they feed on refuse. It is possible that the bee or wasp-like aspect of the *Volucella* may serve as a protection against an attack by the workers of the community. Sladen has noticed that the female *Volucella bombylans* continues to lay eggs after receiving fatal injury, and has suggested that this power of partial survival may enable an invading fly, detected and stung by a bumble-bee, to ensure, notwithstanding her own speedy death, the development of her offspring.

It is well known that a very large proportion of the nests of solitary wasps and bees are invaded by females of other wasps and bees for the purpose of egg-laying, and the grubs, as soon as hatched, begin to feed on the store provided by the rightful owner for her own offspring, which may conse-

quently die of starvation. Such insects, thus taking advantage of the labours of others, are known as inquilines or "cuckoo-parasites." In some cases the inquiline larva devours the grub of the host, behaving like a beast of prey, having by its mother's action been insinuated into the habitation of its victims. The origin of these types of parasitism among the sting-bearing Hymenoptera (Aculeata) has been suggestively discussed by W. M. Wheeler (1919), who gives good reason for believing that the parasitic habit arose in all cases among members of the same species, whereof in times of "scarcity of prey or food . . . individuals . . . might find it as easy as advantageous to steal the provisions of other individuals." Wheeler suggests further that the urgency of the egg-laying reflex would reinforce the stimulus due to scarcity in tending to establish the parasitic habit. He insists that many of the inquiline Hymenoptera now distinguishable specifically and often generically from their hosts, are nevertheless closely related to the latter, and the habit as developed among social bees and wasps affords strong evidence in support of this view.

In communities of bumble-bees it has been shown by F. W. L. Sladen (1912) that occasional or incipient parasitism is fairly common. One queen may enter the nest of another of the same kind, kill her and install herself in the vacant place. Among our British species are two nearly related, *Bombus terrestris* and *B. lucorum*, the former of which not infrequently preys on the latter, "killing the *lucorum* queen and getting the *lucorum* workers to rear her [own] young." This habit is, of course, abnormal and occasional, but it might easily become the starting-point for a definitely parasitic race. Its further development is illustrated by the peculiar inquiline bumble-bees of the genus *Psithyrus*, which have no worker-caste and whose queens are destitute of the characteristic pollen-gathering structures on the hind-legs. An over-wintered female of *Psithyrus* enters a young nest of *Bombus* in the spring after the first set of the workers have been developed. She seeks "to ingratiate herself with the inhabitants, and in this



FIG. 60A.—Queen-Wasp (*Vespa austriaca*).  $\times 3$ .

she succeeds so well that the workers soon cease to show any hostility towards her." After a time she kills the *Bombus* queen, thereby cutting off any further production of workers, but those already in the nest are enough for the tendance of the intruder's eggs to which and to the resulting larvae the workers "soon get reconciled" so that "they feed and tend the *Psithyrus* brood with as much devotion as if it were their own species." Sladen insists that the resemblance of a *Psithyrus* to a *Bombus* "is not merely superficial but extends to nearly all the important details of structure, so that it is impossible to avoid the conclusion that *Psithyrus* has sprung from *Bombus*, and this at quite a recent period in the history of life." Here we find the inquiline specialised in such a way as to bring the invading queen into definite social contact with the host-workers, so that these—not through any motive that can be truly called "devotion," but as a result of their normal, inherited reflex tendencies—feed her young as though they were their own sisters.

Among the social wasps (*Vespa*) there are several species



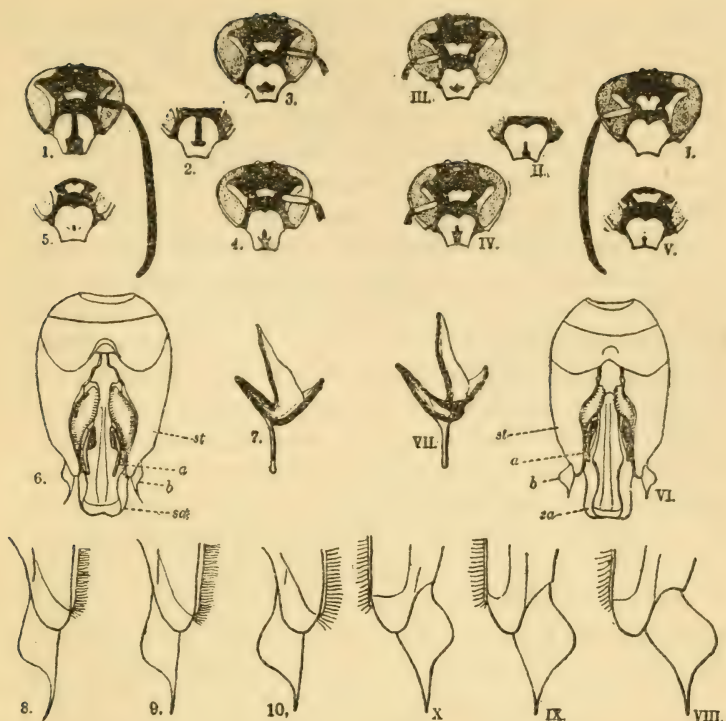


FIG. 60B.—*Vespa rufa* and *V. austriaca*. 1, Face of typical male *V. rufa*; I., face of typical male *V. austriaca*; 2-5, series of male *rufa* faces approaching *austriaca*,  $\times 4$ . 6, Male armature of *V. rufa* (ventral view); VI., of *V. austriaca*; (st, stipes; sa, sagittae; a, internal, b, terminal process of stipes),  $\times 8$ . 7, internal stipital process of male *V. rufa*; VII., of *V. austriaca*,  $\times 16$ . 8, Terminal stipital process of typical *V. rufa*; VIII., of *V. austriaca*; 9 and 10 of *rufa* approaching *austriaca*; IX. and X., of *austriaca* approaching *rufa*,  $\times 28$ . After H. G. Cuthbert (*Irish Nat.* vi. 1897) and Carpenter and Pack-Beresford (*Ib.* xii, 1903).

of which no workers are certainly known, such as *V. austriaca* (Figs. 60A and 60B) in Europe including the British Islands, and *V. arctica* in boreal North America. It has been well known, since the observations of J. W. Robson (1898), that queens and males of *V. austriaca* are reared in nests of the common *V. rufa*, to which it is generally believed to stand in the relation of inquiline to host. The American *V. arctica* is

reared, according to Wheeler and others, by workers of *V. diabolica*. The systematic relationship between these apparently "cuckoo" wasps and their hosts is exceedingly close, much closer than that between *Pysithrus* and *Bombus*. G. H. Carpenter and D. R. Pack-Beresford (1903) showed from a study of the male armature and the variation of coloration and structural features in *V. austriaca* and *V. rufa* that these two species are much more nearly related mutually than either is to any other British wasp, and that each of the two forms varies towards the other as regards these characters (Fig. 60B, I-10 and I.-X.). From a census of the population of a nest in which the old queen was an *austriaca* and the latest emerged members workers and males of *rufa*, these observers concluded that the two might reasonably be regarded as alternative forms of one variable species, since an *austriaca* queen was apparently the mother of individuals which were clearly referable to *rufa*. Yet the occasional inquiline habit of one race of *Bombus* on another, mentioned already in this chapter, lends support to the accepted view that *Vespa austriaca* frequently plays the part of a cuckoo-parasite on *V. rufa*. Certainly all the facts combine to confirm Wheeler's generalisation that inquilines among the aculeate Hymenoptera are always nearly related to and genetically derived from their hosts.

Turning from wasps and bees to ants, we come to consider the most remarkable of all social insects—in some respects indeed the most remarkable of social animals, for the ant-community may be organised and specialised, within the limits imposed by the structural and psychic conditions of its members, to a degree that challenges comparison with the human commonwealth, so that the activities of ants have been held up by moralists as an example to encourage industrious effort among men. Modern students of the ways of ants have the great advantage of being able to consult the comprehensive treatises of W. M. Wheeler (1910, see also 1923 and 1926) and A. Forel (1921), while the habits of our British species have been well described by H. K. Donisthorpe (1927).

Among ants all the species are social, and members of the worker caste are sharply differentiated by complete winglessness; while they show the highly developed structural features of their order, with modifications fitting them for the specialised activities of their lives, wings are never developed in the course of their transformation. Hence the worker-ants are more strongly differentiated from their fertile sisters than worker wasps and bees are; and in many groups there may be recognised, among the wingless infertile females, two or more distinct forms divergent from each other in size and often in structure, while among the fertile females (queens) as well as the males, separate castes may in some cases be distinguished. The winglessness of worker-ants is matched by the females of many non-social Hymenoptera, species of gallflies and members of groups with parasitic larvae, for example. Among the Scolioids, believed by Wheeler and others to represent the ancestral stock of true ants, there are two small families—the Thynnidae and Mutillidae—whose females are wingless. It seems, therefore, that this condition may have arisen independently in a number of groups among the Hymenoptera, and that it has become a fixed character among all the ant workers. It is suggestive to remember that in the workers of certain species of ant, vestiges of wings may occasionally be detected. Quite a number of abnormal forms of queens tending to resemble workers and also forms of worker more or less resembling queens have been described and provided with special names for which reference may be made to Wheeler's book (1910). Some of these worker-like ("ergatoid") queens are wingless like the workers. It is well known that all ant-queens after the nuptial flight shed their wings; only by the persistent bases of these can the queen in a nest be recognised as an insect once able to rise in the air. The flight-muscles of the wingless queen, now no longer required, undergo a rapid degenerative process described in detail by C. Janet (1907). These muscles, "the most voluminous of all the organs of the body, experience a precocious senescence,"



suffer interruption of their innervation, and undergo a solvent action by ferments present in the blood.

Among ants generally a new community arises, as among social wasps and bumble-bees, by a young queen starting a new nest, and herself doing all necessary work, rearing the grubs and feeding them with her own spittle, as she does not leave the nest until the first brood of workers are developed ; then these take on the labours of the society. In some cases, however, daughter-queens may return, after the nuptial flight, to their native nest which thus comes to harbour a number of fertile females all helping to increase the size of the family. Again such a many-mothered (polygynic) society may give off colonies consisting of young queens "each accompanied by a detachment of workers." The variety of method shown by ants in producing new family societies is of great interest, suggesting that their behaviour is more plastic and less stereotyped than that of most other social insects.

The wingless condition of the worker-ants is correlated with their prevalent habit of nesting in the soil ; the vast majority of members of this family may be reckoned among those insects which have abandoned aerial life for an existence mainly terrestrial. With this mode of life are associated many adaptations of structure well known to observers at all familiar with the aspect of worker-ants. Their eyes are usually small, while their elongate feelers well provided with tactile and olfactory sense-organs are in constant use. Their long slender legs are well suited for the rapid running which goes far to compensate for the loss of flight. Wheeler dwells on the "very long and intimate contact with the soil" which "has made the ants singularly plastic in their nesting habits," while A. Espinas (1877) pointed out that the loss of the power of flight among worker-ants is not without compensation in the increased intelligence partly at least attributable to their terrestrial life. "On the earth . . . there is not a movement that is not a contact and does not yield precise information, not a journey that fails to leave some reminiscence."

Among many ants of the same species the workers of a community differ among themselves so that two or more definite types or castes are recognisable. These are usually adapted for performing special functions in the social life so that the communities practise a "division of labour." For example, there may be workers with abnormally large heads armed with powerful mandibles; such in some societies are the so-called "soldiers," "policemen or defenders of the colony," while in certain harvesting or hunting ants their work is "to crush seed or the hard parts of insects so that the softer parts may be exposed and eaten by the smaller individuals." Among the well-known "leaf-cutting ants" of the American tropics (*Atta* and allied genera), whose object in collecting and dividing the leaves was first detected by T. Belt (1874) as the provision of a soil on which to raise in the underground chambers of their nests the fungi on which they feed, there are in many species large-headed workers which carry out the spectacular raiding expeditions in the forests and bear away the leaves into the nests, where smaller workers with heads of normal form act as "mushroom-gardeners" in the deeply situated cavities where the food of the community is actually grown. A striking feature noticeable in most ant communities is the close correspondence between the modifications of the workers and the nature of the food. Among the "legionary" or "driver" ants—which include the African and Oriental *Dorylus* (Fig. 61) and *Anomma*, and the tropical American *Eciton* and allies—the communities range over the country often in huge swarms attacking insects, spiders and sometimes even large vertebrates which furnish their food. The workers are blind, guided on their forays through their senses of touch and smell, varying greatly in size, the larger castes with great broad heads, armed with long trenchant mandibles. The picturesque account of T. S. Savage (1847) has been confirmed by later observers. He described "an arch for the protection of the [smaller] workers constructed of the bodies of their largest class," whose "widely extended jaws, long slender wings and

projecting antennae intertwining form a sort of network." He watched these driver ants hang together so as to form "festoons or lines of the size of a man's thumb," reaching from the lower branches of trees to the undergrowth. Across such living bridges other ants can pass to and fro, up or down. Savage saw "one of these festoons in the act of formation . . . ant after ant coming down from above, extending their long limbs and opening wide their jaws gradually lengthening out the living chain until it touched the broad leaf of a *Canna* below." As the festoon of ants

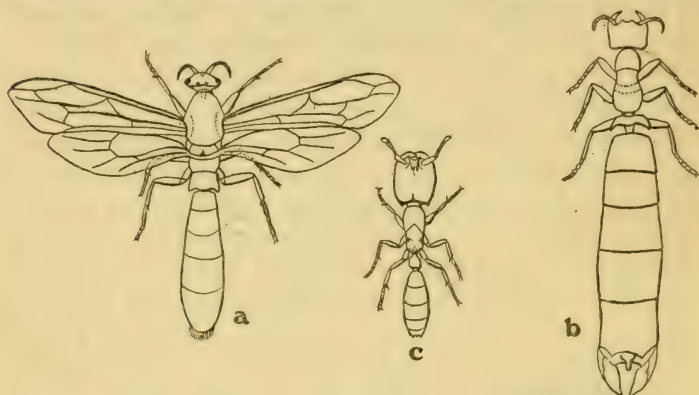


FIG. 61.—South African "Driver" Ants. *a*, *Dorylus fulvus*, male,  $\times 3$ ; *b*, *D. fimbriatus*, female (queen after casting wings),  $\times 3$ ; *c*, *D. fulvus*, worker,  $\times 2$ . After G. Arnold (*Ann. S. Afr. Mus.* xiv, 1916).

swung in the wind, the lowest ant tried to lay hold of the leaf with feet or jaws without success, whereupon a large worker climbed up on the leaf from below and "fixing hind-legs with the apex of the abdomen firmly to the leaf," reached upwards with her front legs and opening wide her jaws, seized the lowest comrade on the chain, "and thus completed the most curious ladder in the world." While the large workers or "soldiers" attack, seize, and bite up the prey, the small members with short mandibles carry the grubs and pupae when on migration. The nests of these driver ants are to a considerable extent temporary. Wheeler



quotes observations on the East African *Anomma molestum*, a community of which "occupies the same nest until it has destroyed all the available prey in the locality," an operation which may occupy "some eight or ten days," then "the colony migrates to a new nest." The fertile females of most Doryline ants are blind and wingless, resembling workers in their structure much more closely than queens. They are, however, when compared with the workers, of relatively enormous size as are also the heavily built males furnished with wings and eyes (Fig. 61).

The feeding habits of these "drivers" seem crude and primitive when compared with the elaborate leaf-cutting and fungus-growing performances of the species of *Atta* previously mentioned. Wheeler believes that the hunting, pastoral, and agricultural modes of life have succeeded one another among ants as they are commonly believed to have done among men. Those ants whose staple food is honey or "honey-dew" illustrate the pastoral stage of society, because their sweet nourishment is obtained largely from the intestines of aphids, scales, and other insects which suck sap from plants. They are often tended and protected by the ants whose behaviour in connection with the "guests" of their societies will be discussed later in this chapter. Many ants, however, go directly to plants and obtain supplies of sweet sap "from small glands or nectaries situated on their leaves or stems, where it is eagerly sought and imbibed" (Wheeler, 1923), or lick up the honey-dew which has been voided by aphids and spread over foliage and shoots. Worker-ants that collect honey or honey-dew have the habit, on returning to the nest, of regurgitating from the crop a portion of what they have swallowed, allowing drops of it to be licked up by those workers which remain in the nest and act as nurses to the larvae, to whom a share of the liquid food is passed on. Ants are incited to disgorge this liquid food when touched or stroked by the feelers of their comrades. Such workers tend therefore to act as temporary reservoirs of food material, and in many groups with this habit (*Camponotus*, *Lasius*, and *Prenolepis*, for example) the

insects' abdomens become capable of considerable distension. This condition is brought to extreme development by the oft-described Mexican honey-ants (*Myrmecocystus*), in the underground chambers of whose nests special workers with immensely swollen abdomens may be found hanging from the roof by their feet, back downwards. These bloated creatures ("repletes") incapable of movement, are fed by the foraging ants in order that they may serve as "honey-pots" for the community as a whole. The abdomen of a replete assumes approximately a globular form, the pale intersegmental cuticle becoming greatly expanded and the normal dark abdominal sclerites appearing on its area as narrow transverse bars. H. McCook (1882), who first carefully investigated the nests of these honey-ants, believed that the repletes are workers definitely adapted for their strange function by the structure and character of their abdominal cuticle and the wall of their food-canal. Wheeler, however, considers that there is no inherited difference between the foraging and the honey-pot workers; the latter are modified if they assume the part of reservoirs when sufficiently young, while their tissues are still plastic, but "thoroughly hardened workers of the ordinary form . . . are no longer able to become repletes."

The most specialised form of behaviour among ants that feed on vegetable substances is probably exhibited by the fungus-gardeners (*Atta*) already mentioned in this chapter (p. 239). The harvesting ants, however, whose activities are celebrated in the writings of Hebrew sages and Greek and Roman poets, display purposive habits hardly less surprising. The ancient accounts of these insects were indeed regarded with no little doubt until the careful observations of T. C. Jerdon (1854) on Indian species of *Pheidole* and *Solenopsis*, and of T. J. Moggridge (1873) on the South European *Messor barbarus* and allied forms, convinced naturalists that the workers of these ants do indeed collect the seeds of plants suitable for food and store them in the underground chambers of their nests. Germination of the harvested grain is prevented by the ants

biting off the radicle, and bringing the seeds in damp weather out of the nest to dry them in the sun. When, as sometimes happens through neglect of these precautions, some of the stored seeds begin to sprout they are carried out of the nest and placed on the surrounding soil to form what may be termed a refuse heap. From such rejected seeds plants may grow up, and the presence of these close to the ants' nests has led some students to the mistaken inference that the insects have deliberately sown the seeds there in the anticipation of a harvest! Much recent information on these fascinating creatures will be found in Wheeler's great book (1910).

All worker-ants feed the larvae of their nests, but Wheeler has recently (1918, 1923) laid stress on the fact that among ants, as among wasps, the feeding is reciprocal. Some ant-grubs, like the wasp-larvae, supply a salivary juice from the mouth to appease the workers that attend on them, but the common habit of the ant-larva is to "sweat a fatty secretion through the general integument of the body." The licking of grubs by the female ants (whether queens or workers) is not therefore to be interpreted as a sign of affection or solicitude but as a method of obtaining attractive liquid food. In ant communities the practice of mutual feeding (trophallaxis) is thus almost universal, not only among the developed adults, but between these and the helpless grubs which they tend.

The larvae of ants are, like those of bees and wasps, legless grubs, but while in the latter groups the larval cuticle is smooth and bare, that of the ant-grubs is usually covered with hairs, which may be simple, forked, hooked, branched, or sawlike and, in some cases, borne on distinct tubercles. The hairiness of ant larvae is definitely suited to their manner of life, as by means of these cuticular outgrowths, the grubs are kept from direct contact with the damp walls of earthen nest galleries, while they are anchored to the walls or to the under surface of covering stones. The hairs of many neighbouring grubs may interlock so as to 'hold the young larvae together in packets,' and enable



the workers "to transport large numbers with little effort," as Wheeler remarks. It is likely also that the hairy covering of an ant-grub protects its body from injury when seized by the jaws of a worker. Most ant-grubs are fed by the workers with disgorged liquid food, and in such the mandibles are feeble. In some groups, however, the grubs are fed on insects and are provided with fairly strong jaws.

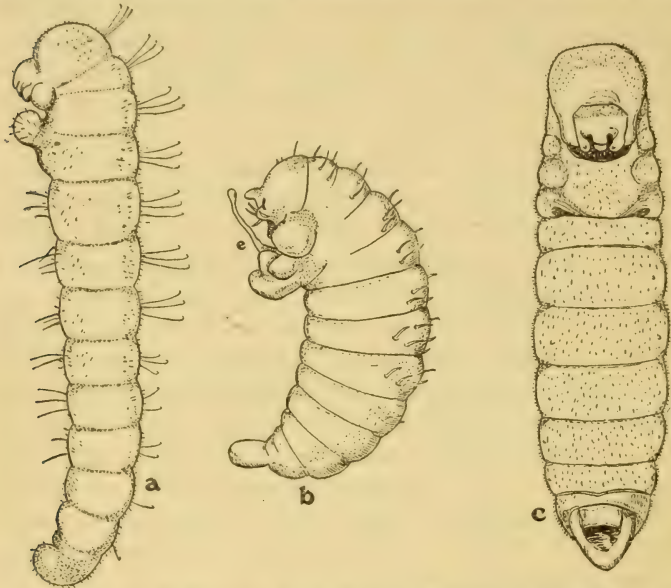


FIG. 62.—*a*, Full-grown larva of Ant, *Tetroponera tessmanni*, West Africa. Side view. *b*, young larva of *Pachysima aethiops*, West Africa. Side view (*e*, exudatorium). *c*, full-grown larva of *P. aethiops*, ventral view. Magnified. After W. M. Wheeler (*Proc. Amer. Phil. Soc.* lvii, 1918).

Wheeler has described (1918) how in certain American Ponerine ants the larvae are fed lying on their backs, the workers depositing bitten-up insects on the ventral surface of the body of each grub, which then pours out a copious salivary secretion; this serves to digest the grub's own meal and to provide a nutritious draught for its nurse. As already mentioned, most ant-larvae exude from the body-surface a sweet fluid which the workers lick up. Wheeler

describes how in the larvae of some African species of *Pachysima* (Fig. 62) there are on the ventral region of the thoracic and first abdominal segments thin-walled finger-like outgrowths in which fat-cells lie near the base while the distal portion of the "exudatorium" contains the clear fluid which, forced out through the body wall, can be conveniently imbibed by the worker as she feeds the grub, the grub's head being so situated as to be surrounded by the curious outgrowths; these become relatively smaller in the later stages of larval life (Fig. 62, *b*, *c*) when the food consists of pellets of insect fragments, the grubs in earlier stages being fed on disgorged fluid.

While the general behaviour of the members of ant communities is mutually helpful, there are occasions when individual self-assertion becomes evident. In times of scarcity workers, especially the larger castes among polymorphic ants, may devour their comrades. Workers, short of food, may eat grubs and pupae instead of tending and protecting them. Between ants of different communities or of different kinds there are various highly interesting possibilities of relation. The driver or legionary ants (p. 240 above) are as ready in their raids to prey upon other ants as on cockroaches, grasshoppers, spiders, or vertebrates. "Certain small but aggressive ants," writes Wheeler, "which secure at least a portion of their sustenance by way-laying the foraging workers of another species and snatching away their food, deserve the name of brigands. Such ants naturally make their nests near those of the species they plunder." Some predaceous species raid the nests of more pacific ants, kill adults and carry off larvae and pupae to serve as food. From such habits as this has arisen, in the opinion of Wheeler and others, the oft-described "slave-making" of *Formica sanguinea* which ranges over all the north temperate regions of the globe, its societies harbouring a number of workers of the allied *F. fusca*. From established communities the *sanguinea* workers go forth to raid nests of *fusca* whence they bring back grubs and pupae, some of which are not killed, but preserved to grow into

workers that share in the labours of the captors. According to Wheeler's observation a young *sanguinea* queen is incapable of establishing a nest of her own; she therefore enters a *fusca* nest, and seizes a number of worker-pupae, killing any *fusca* workers that seek to interfere with her. The gang of workers she has annexed begin as soon as they have emerged to feed her and tend the grubs hatched from her eggs. The *sanguinea* workers reared from these have the inherited instinct to raid nests of *fusca* and capture larvae and pupae; thus a mixed community is formed, the workers of the two species sharing in the common labour.

Communities of *Formica fusca* suffer also from raids by "Amazon Ants" (*Polyergus*), oppressors more formidable than *F. sanguinea*. There are several species of *Polyergus*, most of them, like the well-known *P. rufescens*, bright red in colour, provided with sharp, slender curved mandibles "perfectly adapted for fighting but of no use for digging in the earth or capturing food." The main facts about the behaviour of these slave-making ants were described more than a century ago by P. Huber (1810), who bestowed on them the suggestive title of "Amazon." Extensive observations on the European forms were subsequently made by Forel (1874), while C. Emery (1911) has given an account of the foundation of a community by the young queen *Polyergus*. She invades a weak nest of *Formica fusca*, kills its queen by biting into her head, and then is adopted by the *fusca* workers, which tend and feed the grubs hatched from the amazon's eggs. The *Polyergus* workers which develop from these have neither the structure nor the instincts to enable them to do the work of the nest or to procure food. Their part is to make raids on other *fusca* nests, where they kill the adults so far as may be necessary for their purpose of carrying off the *fusca* larvae and cocoons to their own nest, the "slave" population of which is thus kept up to the necessary level. The Amazons are, as has frequently been remarked, "absolutely dependent on their slaves" for the maintenance of the community and the survival of the race. Wheeler comments on their "two



contrasting sets of instincts. While in the home nest they sit about in stolid idleness or pass the long hours begging their slaves for food or cleaning themselves and burnishing their ruddy armour ; but when outside the nest on one of their predatory expeditions they display a dazzling courage and capacity for concerted action compared with which the raids of *sanguinea* resemble the clumsy efforts of a lot of untrained militia." The Amazons make their raids always in the afternoon hours and Forel actually observed forty-four raids on thirty afternoons during a period of seven weeks after midsummer. He estimated the number of amazon workers at 1000, and of the pupae captured by them during the summer at 40,000. But only a small proportion of these develop into slaves ; many are killed and eaten by the Amazons while others are accidentally and fatally injured in transport.

Contrasted with these slave-making instincts are the ways of certain ants which Wheeler defines as temporary or permanent " social parasites." Communities of the former group arise through the adoption of a young queen in a nest of the host ants. F. Santschi (1920) describes how a newly hatched female of the North African *Bothriomyrmex decapitans* is " arrested " by workers of *Tapinoma nigerrimum* when she approaches their nest, and dragged inside. If any denizen threatens attack, she gets among the host-larvae or on the back of the host-queen ; in such situations her own characteristic odour is masked by that of the native insects. The invader while on the back of the *Tapinoma* queen may employ herself in biting off the latter's head (hence the specific name, *decapitans*). The *Bothriomyrmex* grubs are tended and fed by the *Tapinoma* workers ; these ultimately die off, and as there is no host-queen left, the mixed community is succeeded by a society composed entirely of *Bothriomyrmex*. This cannot be started without the help of *Tapinoma*, but when established it can carry on independently, so that the parasitism is temporary.

Among the permanent social parasites there is no worker caste. The European *Anergates atratulus* inhabits nests of

*Tetramorium cespitum* ; its habits are described by Forel (1874), Janet (1897), Wheeler (1910), and others. The males are wingless, and pairing must therefore take place in the nest of *Tetramorium*, whence the young winged females emerge in summer, and after casting their wings, enter other *Tetramorium* nests, where they are received by the workers, which ultimately kill their own queen and devote themselves to attendance on the *Anergates* grubs. The *Anergates* queen displays, as her eggs develop, a greatly swollen abdomen, on which the sclerites become widely separated by tracts of pale flexible cuticle, as in a "replete" worker honey-ant or a queen-termite. The *Tetramorium* community that harbours *Anergates* must ultimately die out since the workers have assassinated their mother. The conditions of the permanent social parasitism among ants are most remarkable both as regards the degeneration of the parasite, and the apparently unnatural behaviour of the host-workers. Wheeler agrees with Emery in considering the mode of life of the temporarily parasitic ants to have been derived from the slave-raiding habit, which seems itself to have arisen as a specialisation of predaceous feeding. The degeneration of habit noticeable in the "slavers" is emphasised among the temporary parasites, while the permanent parasites have no longer a worker caste. Wheeler calls attention to the extreme rarity of species of the last group ; they are "so very scarce that they must be on the very verge of extinction—a fact which shows that parasitism, so far as race is concerned, is anything but a promising or profitable business." It is noteworthy that nearly all the slavers and social parasites among the ants are closely related to their hosts, as the parasitic wasps and bees are, so that for the ants also that practise such habits we may infer a common origin with the creatures which they oppress or exploit.

Ants, more than all other insects, furnish examples, numerous and varied, of association with insects of other orders and creatures of other animal classes which inhabit their nests and share in their social life as guests of the com-

munity. Such "myrmecophiles" have been extensively studied in recent years, and for details as to their relations to ants the writings of E. Wasmann (1920) may be advantageously consulted. Many of the ant guests contribute nutrient material on which the ants feed. Of these the aphids ("greenfly") and some allied Hemiptera are the best known. As previously mentioned in this chapter (p. 241), the aphids, sucking sap in great quantity from plants, void from their intestines drops of the surplus food substance, of which they can use but a small proportion for their own sustenance. The fluid evacuated by the aphids is therefore not excreted waste-matter but digested fluid food in which much of the sugar has undergone inversion. Aphids therefore furnish an extensive and convenient source of food supply to the large proportion of ants that live principally or entirely on "honey-dew." To obtain the liquid ants may follow the "greenfly" as they feed on plant-shoots, or, in the case of root-sucking aphids, harbour them in their nests. Ants in attendance on aphids may be observed stroking them with feelers or fore-legs, and the aphids in response exude drops of honey-dew which the ants swallow.

Besides aphids, scale insects and mealy bugs (Coccidae) and sucking insects (Homoptera) of other allied families are harboured by ants for the sake of the honey-dew voided from their intestines. There are many records of the care taken by the various kinds of worker-ants of young, newborn aphids, root-sucking kinds being carried by the ants to fresh rootlets especially soft and succulent. While such underground aphids are herded by their ant guardians within specially constructed earthen "pens," some aphids and coccids that feed on the shoots of plants are gathered into droves by the ants, which build over them covers of silky or papery substance beneath which they are protected and sheltered. Wheeler points out that certain features of structure and behaviour observable in these ants that feed on honey-dew and in the sucking insects that supply their food, confirm the opinion that the relation between the



two kinds of insect is mutually beneficial. Ants that use aphids in this way, as "cattle," never devour or attack them; they rather protect them and drive off threatening enemies or carry away the aphids to some safe refuge. The aphids, on their side, never try "to escape from the ants . . . but accept the presence of these attendants as a matter of course." A. Mordwilko (1907) states that in some aphids habitually associated with ants, there is a ring of stiff hairs surrounding the vent; these hairs hold the drop of honeydew until the feeding ant has swallowed it, so that they appear to be related rather to the latter than to the aphid itself.

Among the most remarkable of all ant-guests are various

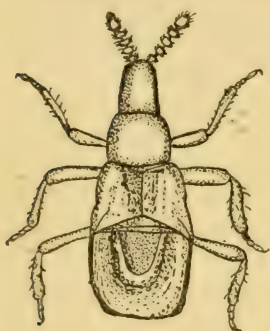


FIG. 63.—Pselaphid Beetle (*Claviger testaceus*) a "guest" of the British and European Yellow Ant (*Lasius flavus*).  $\times 12$ .

kinds of beetles that spend their whole lives in ants' nests. They belong to several distinct families, such as Staphylinidae or rove-beetles and their allies the Pselaphidae (Fig. 63), as well as the curious Paussidae. Wasmann has described and discussed at length the relations between the ants and these guest-beetles which are frequently reddish in colour, their bodies adorned with tufts of yellow hairs surrounding the openings of glands which secrete an aromatic volatile fluid licked

up by the ants. The beetles are themselves fed by the ants on disgorged liquid; the guests solicit this by stroking with their feelers or fore-legs the heads of their hosts. Their jaws are often modified for the reception of this liquid food, so different from the solid nutriment devoured by the vast majority of beetles. Not the adult beetles only but their grubs also live in the ants' nests, where they are tended and fed by the workers, though they have often been observed to attack and devour the ant larvae. It has not unnaturally been suggested that the ants

which harbour these guests "care more" for the beetle grubs than for their own. But this mode of expression attributes to the ants motives for behaviour which do not necessarily follow from the observed actions, for it is very doubtful how far the worker-ants, whose responses are mostly made to tactile and olfactory stimulations, distinguish between the various inmates in the nest with which they come into touch. A creature, be it sister-ant or guest-beetle, which gives the tap on the head to which the normal response is regurgitation of food, is fed as a matter of course by any worker in the nest.

This conclusion is supported by the relation between several species of *Lasius* and certain tiny mites (*Antennophorus*) which are carried about and fed by the worker-ants although, unlike most of the guest-beetles, they furnish the ants with no food substance in recompense. Janet (1897) has described how a worker may be observed to carry along the galleries of an underground nest of *Lasius*, three of these mites, one with its back downwards clinging to the ant's neck with its three hinder pairs of feet, and the other two holding on one on either side of her abdomen. The long front legs of the *Antennophorus* are used to tap the head of an ant so as to obtain in response a drop of honey; evidently the mite carried beneath the ant's head can obtain the boon readily and directly from its bearer, while those mites which cling to an ant's abdomen depend for their supplies of food on other ants, which they touch in the course of their journeys through the nest galleries. It might be imagined that the ants would not carry about and feed these useless guests unless some feeling of satisfaction were to result from the act, comparable, for example, to the gratification many human creatures seem to derive from carrying about and feeding useless small dogs and kittens. But these mite-harbours ants have really no goodwill towards their tiny guests, for when a mite first attaches itself the ant-carrier tries to shake it off, and the act of feeding in response to the tap of the little creature's foot, is a simple and inevitable reflex.

Another method of obtaining food is practised on *Lasius mixtus* by a small bristle-tail (*Atelura*) found in numbers in the ants' nests. Janet (1896) describes how when one worker-ant is disgorging honey to feed a comrade, the *Atelura* thrusts itself between the two, "raises its head, snaps up the droplet, and makes off at once as if to escape merited pursuit." This action might be naturally described as thieving; the little bristle-tails lurk in the nest where they find shelter and take any opportunity of seizing food. A more specialised method of exploiting ants is practised by the maggots of a Texan fly (*Metopina*) described by Wheeler as "messmates" in the nest of a species of *Pachycondyla*, which feeds its larvae with fragments of insects, these being placed by the workers on the concave ventral surface of the grub within reach of its jaws. Each maggot of *Metopina* coils itself around the neck-region of the ant-grub, and whenever the latter receives its allowance of insect fragments, the fly-larva "uncoils its body and partakes of the feast." Both "host" and "guest" become full fed about the same time, and the latter, enclosed in the former's cocoon, retires for pupation to the tail end of the ant-grub, which completes its transformation before the fly-maggot, and on emergence from its cocoon leaves an opening through which the fly when subsequently developed can make its way out.

Many more examples might be given of creatures of other kinds that share the life of the ant communities. The nature of the association varies immensely. On the one hand, we notice the mutually beneficial activities of ants with aphids or with various caterpillars belonging to blue (*Lycaenid*) butterflies; these produce from a dorsal gland opening on the sixth abdominal segment, a sweet fluid acceptable to the ants which follow the caterpillars about on plants or harbour them in their nests. On the other hand, there are mere thieves like the bristle-tails, mites, and *Metopina* maggots, or "insect jackals" like certain rove-beetles that devour dead, decrepid and feeble ants, or attack and prey on solitary active ones. Wheeler well



describes them as a "perplexing assemblage of assassins, scavengers, satellites, guests, commensals, and parasites."

Wasps, bees, and ants, among which are included the vast majority of social insects, belong to the Hymenoptera, one of the most highly specialised of all the orders of the insect class. It is, however, of great interest to find that an elaborate social life, depending on the growth of an enormous family, is characteristic of a lowly organised group—the Termites, which though often called "white ants," have no near relationship to true ants, but belong to a comparatively primitive order, the Isoptera. Among the Embiidae, a tropical and sub-tropical family closely akin to the termites, there is to be noticed an incipiently social habit analogous to that characterising some of the "solitary" wasps and bees. Many male embiids are winged; the wingless females tend their eggs and young much as the mother-earwig (p. 210) cares for her brood. A. D. Imms (1913) describes how in the Himalayan *Embia major*, "when the young larvae are hatched, they remain around the parent female, who conceals them, so far as she is able by means of her body." These insects spin, from glands situated in the fore-feet, an abundance of silken thread, and thus construct extensive webs and galleries in which their families carry on a primitive community life. All the adults among the Embiidae are normal fertile males or females; there is no worker caste.

In a termite society, on the other hand, the immense majority of members are infertile, wingless "workers" (Fig. 64, *d*) with small heads and jaws, together with a smaller though considerable number of larger-headed, long-jawed "soldiers" (Fig. 64, *c*). While in the bee or ant community all the infertile insects are females, the worker and soldier castes among the termites may belong to either sex. The differences between the various members of a termite society were formerly believed to be induced by differences in feeding, but the researches of E. Bugnion (1913) and Caroline B. Thompson (1916) have demonstrated that, at least in some cases, the caste characters of

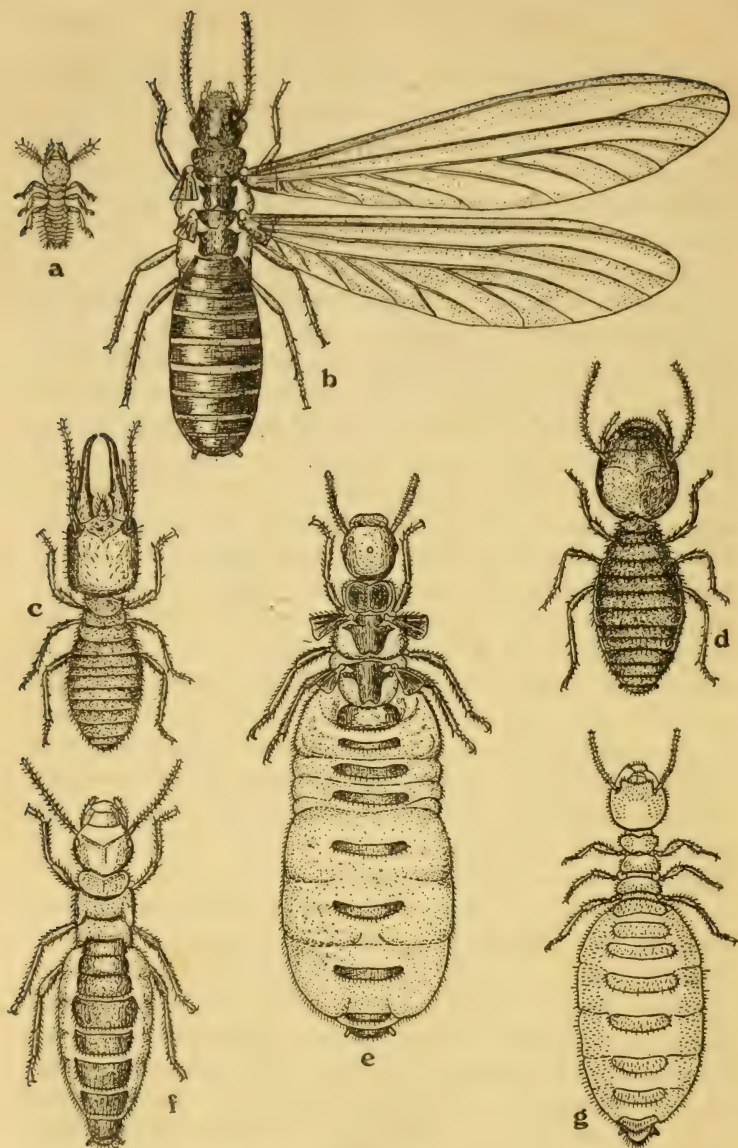


FIG. 64.—Forms of Termites, North America. *a*, Larva of *Leucotermes flavipes*,  $\times 8$ , after C. L. Marlatt (U.S.D. A. Ent. Bull. 4); *b*, male of *Amitermes tubiformans* (left wings cast),  $\times 10$ ; *c*, soldier, and *d*, worker, of *A. arizonensis*,  $\times 10$ ; *e*, “queen” of *Leucotermes flavipes*,  $\times 16$ ; *f*, second form, and *g*, third form female of *L. tibialis*,  $\times 8$ . After N. Banks and T. E. Snyder (Bull 10 U.S. Nat. Mus. 1920).

termites are definitely inherited, as among the newly hatched young two sets of individuals may be detected, some with smaller brain, eyes, and reproductive organs destined to become workers or soldiers, while others with those structures normal, develop into fertile insects. It is therefore not unlikely that the caste of any termite is determined by the nuclear constitution of the egg whence it arises. Workers and also soldiers of the same species may differ in size, and many termite communities have three distinct forms of fertile males and females. The "kings" (Fig. 64, *b*) and "queens" are winged insects with firm dark cuticle; swarms of them when mature leave their native nests and, after flying for some distance, come to the ground and shed their wings. Many of such swarms are devoured by birds and other creatures; the survivors associate in couples, a male and female, excavating, by their common labour, the rudiment of a new nest in form of a small underground chamber where they pair and start the foundation of a community. In members of the second fertile caste (Fig. 64, *f*) the wings remain undeveloped though recognisable in a rudimentary condition, while the cuticle of the body is feeble and pale. The third fertile caste (Fig. 64, *g*) is characterised by a very pale cuticle and the total absence of wings, features which recall the condition of the workers. It is doubtful if these second and third castes of fertile termites ever leave their native nests; they have been termed "substitution royalties," under the impression that they are kept as "understudies" for the "royalties" in case of disaster to the latter. Termites are among those more primitive insects in which there is no marked transformation in the course of growth, such as is so conspicuous in all the social Hymenoptera, with their pale legless grubs. The newly hatched termite displays all the essential features of its parent, and the adult worker, wingless, soft-coated and pale, with its reproductive system undeveloped, may be regarded as retaining to a great extent the characters of the young. The same view may be fairly taken of the third-form fertile ("neoteinic") termite in which no traces of



wings appear. The soldier termites also remain wingless, and are in that respect undeveloped and youthful in their character; but their heads are highly modified, large with firm, brown capsule, either bearing extremely prominent trenchant mandibles or prolonged into a snout-like process with a repellant gland opening at its tip. They are the defenders of the termite society. It is believed that from eggs of the third-form females, fertile insects like themselves as well as workers and soldiers can be developed. The second-form fertile termites may be parents of members of their own and of the three "lower" castes. Only the kings and queens can give rise to all the varied forms of their kind. When exceptionally a worker or a soldier becomes fertile, it can reproduce its own caste only.

The fertile female termites, in whose bodies numerous eggs are developing, tend to become swollen in the abdominal region, tracts of pale cuticle showing between the darker sclerites, as the integument is stretched. In most "queens" (Fig. 64, *e*) this process is carried to an extreme degree, the swollen abdomen becoming seven or eight times as long as the rest of the body, with its area almost entirely composed of tense whitish cuticle. Thus, while a pair of termites starting a new nest are of the same size, it comes to pass that in some species the "physogastric" queen is four times as long and a hundred times as bulky as her mate, and perhaps fifteen times as long and three thousand times as bulky as her worker offspring. K. Escherich, in his excellent account (1909) of the termites, reckons that a queen of the tropical African *Termes bellicosus* lays about thirty thousand eggs a day, a rate of reproduction which would work out to ten million eggs a year, and to a hundred million eggs in the average ten-year life of one of these insects. He concludes, therefore, that such termite queens must be regarded as the most fruitful females in the whole animal kingdom.

The staple food of termites is wood, and the damage which these insects do to timber structures is too well known to dwellers in tropical and sub-tropical regions. The

workers swallow and digest food and then disgorge it in order to feed the "royalties" and young in their nests. Termites also devour each other's excrement. They build earthen tunnels over exposed surfaces of wood on which they are feeding, and most species are, like ants, predominantly subterranean in habit. Hence particles of soil, as well as wood, are constantly used as food. It is of great interest also to find that many termites, like the leaf-cutting ants already mentioned in this chapter (p. 242), are "fungus-gardeners" and carry on this very specialised method of feeding to as great an extent as the true ants. Wheeler remarks (1923, p. 270) that while the ant mushroom-gardeners "are all confined to a single Myrmicine tribe and are exclusively American, the fungus-growing termites all belong to a few genera . . . and are confined to the Ethiopian and Indo-Malayan regions." In the chambers of their nests the worker termites construct spongy "mushroom beds" consisting of wood and other vegetable material which has been broken up and passed through the insects' food canals. The "fungus-gardens," remarks Wheeler, "are really the nurseries of the termitarium, and are full of just hatched young, which crop the food-bodies like so many little snow-white sheep." The cultivated fungus is not eaten by the developed workers and soldiers; it is a special food provided for the growing young, for the "royalties" and for other fertile members of the community.

Termites, like ants and wasps, practise extensively mutual feeding. Besides the disgorged, digested food and excrement already mentioned, these insects produce exudate substances, derived from the blood and fat-body, which, permeating the thin-body wall and cuticle of the abdomen, can be "licked up by other members of the colony." This habit was observed by N. Holmgren (1909) and K. Escherich (1911), the latter stating that the large swollen queen produces more abundant and richer exudate than any other members of the community, and that her attendant workers in order to obtain the delicacy take the liberty of biting through the royal skin. Wheeler dwells on the importance

of this "trophallaxis" among the termites, as among the ants and wasps, in promoting social life. The habit is even more elaborately developed in termite than in ant and wasp communities; the termites "may be said to be bound together by a circulating medium of glandular secretions, fatty exudates, and partly and wholly digested food, just as the cells of the body of a higher animal are bound together as a syntrophic whole by means of the circulating blood."

Termites of different kinds show much variety of habit in the construction of their nests. The small communities of more primitive forms live in irregular galleries or tunnels excavated in wood or soil. A. D. Imms (1919), in his account of the Himalayan *Archotermopsis*, describes the tunnels made by these insects in fallen trunks and logs of deodar, and comments on "the complete absence of anything in the nature of a true nest or termitarium." Many of the "white-ants" that are notorious as destroyers of timber buildings or furniture, such as the American *Leucotermes flavipes*, inhabit cavities eaten out in dry wood. The "concentrated" nests of more highly organised termites, begun in the underground chamber excavated by the royal pair, are developed through the excavation of surrounding galleries and small chambers by the workers, and completed through the up-building of a broad sloping mound or a steep conspicuous "hill-nest," which may attain a height of fifteen or eighteen feet in the case of several tropical African species, while the nests of some Australian termites, twenty or twenty-five feet high, have been claimed as the largest of all animal dwellings, if the work of human builders be left out of account. The material of the above-ground structure of these hill nests, like that of the earthen tunnels built by many termites over the stems and branches of trees and shrubs, is soil moistened with the termites' spittle, or disgorged or evacuated after being swallowed, and thus brought into condition suitable for use as building material. "On drying," remarks Wheeler, "the substances employed, especially the saliva-impregnated earth, become almost as hard as cement." Wood also, after



treatment with the digestive juices, is used by many termites for the construction of their nests, which, in such case, assume a carton-like consistency. These are often found suspended from the branches of trees, they are particularly characteristic of the tropical American forests, "and vary from the size of a football to that of a barrel." The nests of termites in their multifarious modifications have been lately described in detail in the treatise of E. Hagh (1922).

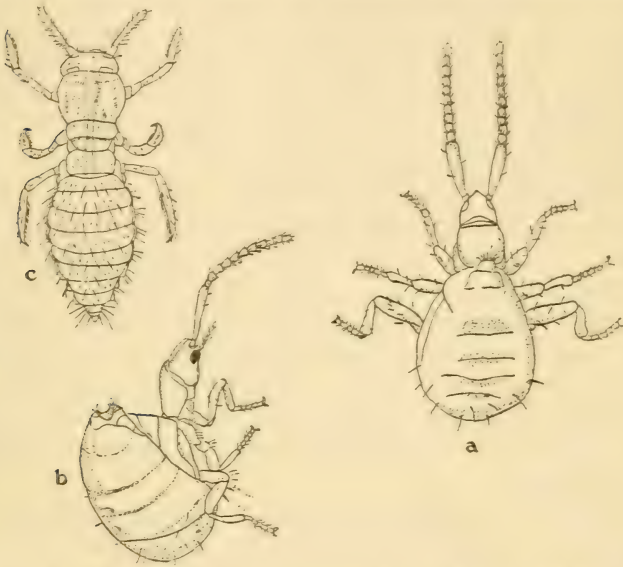


FIG. 65.—Rove-beetle (*Termitoptocinus australiensis*). *a*, dorsal, and *b*, lateral views,  $\times 10$ ; *c*, larva, dorsal view,  $\times 12$ . "Guests" of *Eutermes fumipennis*, N. Australia. After F. Silvestri (*Boll. Lab. Portici*, xv, 1921).

Like the societies of true ants, the termite communities are remarkably interesting on account of the number and variety of alien insects which they harbour as "guests." Our knowledge of these is largely due to the researches of E. Wasmann (1910-12). Many of them are rove-beetles (Staphylinidae), which, like the fertile termites, have assumed the "physogastric" condition, the abdomen being greatly swollen and covered for the most part with soft flexible

cuticle, while membranous areas of the thorax grow out into bladder-like or finger-like processes (exudatoria). This curiously degenerative condition, due to overgrowth of the fat-body, brings the beetles into direct feeding relation with their termite hosts, as the insects can all obtain and swallow exudations from each others' swollen bodies. It is noteworthy that the larvae of these "termitophile" rove-beetles (Fig. 65, *a*) are of a primitive relatively long-legged insectan type, resembling in aspect the young termites (Fig. 64, *a*) whose quarters they share. Very remarkable among the termites' guests are certain abnormal flies (Diptera) like the beetles with swollen abdomens and with their wings reduced to strap-like vestiges. Of these the African and Indian *Termitoxenia* and *Termitomyia* are described by Wasmann (1900), the African *Ptochomyia* (1920) and the Brazilian *Termitomastus* (1901) by F. Silvestri. These are clearly related to well-known families of Diptera (Phoridae and others), of normal structure and with well-developed wings, but all have undergone degenerative modification in correspondence with their dependent life in the termites' nests. Wasmann believes that in *Termitoxenia* the larval and pupal stages have been eliminated from the life-history and that an imago is hatched from the egg.

Early in this chapter (p. 218) it was suggested that in an advanced insect community the individuality of the single bee or ant might be regarded as merged in a greater individuality of the society. This view has been forcibly advocated by Julian Huxley (1912) in a general discussion on the Individual in the Animal Kingdom. "Communities of ants and bees are," according to him, "undoubted individuals"; the single insects are so modified as to exhibit a differentiation of structure and function corresponding to the "division of labour" among the organs of an animal body; one single ant or bee apart from her comrades is incapable of prolonged survival, and owing to the development of the insectan nervous system the ant society is "an individual . . . whose parts, though not contiguous in space,

are yet bound together as fast as the cells of a sponge or the persons of a Siphonophoran." On this view of the matter a single ant cannot be defined as an "actual individual," though "morphologically and historically equivalent" thereto. The members of the community are now "functioning as parts, but descended from ancestors that functioned as wholes." A similar line of argument has been advanced also by W.N. Wheeler (1911) in his discussion on the "Ant Colony as an Organism." He dwells on the community as an organic system in relation, as a whole, with its environment, and in this social organism, the fertile members stand for the germ-cells, the workers and soldiers for the body. H. Bergson (1907) claimed that a bee-community is "really and not metaphorically a unique organism."

This manner of regarding an insect society is analogous to the personification of such a human society as the city or state. In our own communities, however, it is very rarely possible to forget the true individuality of the single member. This may be overlooked in the ants' nests or the bee-hive, because the behaviour of each single insect is so largely determined by inherited reflexes all tending to the maintenance of the community-life, that the single insect ceases to count. The general perfection of this pre-determined behaviour makes the communistic ant or wasp less plastic and originative than the "solitary" members of her family often are. Yet worker insects, confronted with unusual conditions, have been observed to behave in a manner demonstrating some power of initiative and adaptation, and the morphologist, considering the problem, will find it hard to deny the true individuality of any one member of an ants' nest, even if he is willing to call the whole society a "super-organism." The parallel and divergent conditions of the insect community as compared with human society present many fascinating problems for consideration ; but the discussion of these must be deferred to our closing pages.



## CHAPTER X

### ADAPTATIONS TO HAUNTS AND SEASONS

REPEATEDLY in the previous chapters of this book, attention has been directed to the adaptation of various kinds of insects in the successive stages of their growth to the surroundings and conditions of their lives. Singly and as a whole, they are admirably fitted to their environment in the wide meaning of that term. We have seen, for example, that the form of their bodies, their legs and wings and the muscles that move these, are adapted to bring about their characteristic movements whether walking, running, leaping, swimming, or flying. Their jaws and digestive canals are suited to the nature of their food whether solid or liquid. They are provided with beautifully constructed sense-organs, and their nerve-centres are so arranged that the impressions received through these organs lead directly to reflex actions appropriate to the conditions under which the creatures find themselves at the time. In our discussion of the growth and transformation of insects after hatching we saw that the differences so frequent and remarkable between adult insects and their larvae may be to some extent explained as modifications which fit the immature creature for life-conditions markedly different from those of its parent. We noticed also that the form and behaviour of an insect in one stage of its development may often suggest a prevision of the conditions of the succeeding stage. The creature is adapted not only for its immediate present needs ; it often prepares in advance for the future events of its life.

The subject of adaptation is of such importance and

interest to the student of insect biology, that it seems advisable to devote, at this stage, a special chapter to the subject, with illustrations of some of the ways in which insects of different groups, in varying stages of their development are found to be definitely fitted for certain haunts or places of abode, and are enabled to survive the seasonal changes of the year.

We may well begin by considering the haunts of insects from a wide viewpoint—that of the geographer. A comparative study of the distribution of various kinds and groups of insects over the surface of the earth shows that while very many are adapted by special modifications of form and habit to a special and restricted environment, others seem capable of adapting themselves to the most diverse conditions so that they range widely over vast areas.

The “Painted Lady” Butterfly (*Pyrameis cardui*), for example, may be found in the most widely separated regions. In many seasons it is abundant in our islands, the large butterflies with their handsome russet, black and white wings flitting along lowland hedgerows or swooping in bold flight over the bare tops of North British and Irish hills. Swarms of the insects migrate northwards in May and June from the Mediterranean district; these lay their eggs on thistles and other plants and the spring caterpillars feed through the summer, transforming in August and September into a second generation of butterflies. These, however, cannot survive the winter in the climate of northern and north-western Europe; thus the butterfly, though its powerful flight and the variety and wide range of the plants on which its larvae feed, enable it every summer to invade thousands of square miles of northern territory and there produce progeny, can never establish itself as a true resident outside those warmer regions, the conditions of which allow it to carry on a succession of three or four life-cycles each year. The species ranges eastward far across Asia into India and Japan, and is found also abundantly in many parts of America. It is therefore abundant, dominant, endued with great power for wide dispersal, but limited in its

adaptability for permanent residence in northern latitudes through its intolerance of the cold or damp of winter.

Other butterflies of the same family (Nymphalidae), however, such as the "Peacock" (*Vanessa io*) and the Small Tortoiseshell (*Aglais urticae*), whose caterpillars feed on nettles, are not only commonly conspicuous members of the British insect fauna, but permanently resident species, because the butterflies of the second or third brood, which emerge from the pupa in autumn, are able to survive the winter in various shelters whither they betake themselves at the onset of cold weather. So strong is the adaptation of *Aglais urticae* to severe climatic conditions that it is a member of the Arctic fauna, a resident in Greenland. In such a case the presence of the insect in the far northern portion of its range is a demonstration of its power to endure extreme severity of climate.

Dragon-flies, as a group, are also remarkable for their strong flight, and many of them occupy a wide range of territory. One of our common British species, *Libellula quadrimaculata*, has a range extending all round the northern hemisphere, and the immense migratory swarms in which it sometimes appears must be an important factor in its distribution. R. J. Tillyard (1917) points out that the large *Pantala flavescens* and some species of the allied *Tamea* "travel far and wide and have overspread the whole of the tropics." He records how an Australian dragon-fly, *Hemicordulia tau*, "has recently colonised Tasmania across a strait two hundred miles wide."

Very different from such strong flying insects as butterflies and dragon-flies are the tiny, lowly wingless springtails (Collembola), many kinds of which may be found in our country beneath stones, under bark, among fallen leaves, or feeding on soft plant-tissues or on decaying vegetable or animal substances. Some of these, despite their small size and feeble cuticle, have an enormously wide range. There is a dark, almost black, species *Achorutes viaticus* (Fig. 66), not more than  $\frac{1}{16}$  in. in length, found commonly all over our islands and able to adapt itself to what seem the



most varied surroundings. Large numbers may often be seen in garden rubbish-heaps and on farm-land around decaying organic matter. Literally myriads have been observed at the sewage outfalls of large towns—whether on the sea-coast as at Dublin, or on the sewage farms around Manchester and other populous cities of northern England. At Edinburgh and elsewhere it has appeared in multitudes on the water drawn from street hydrants, and

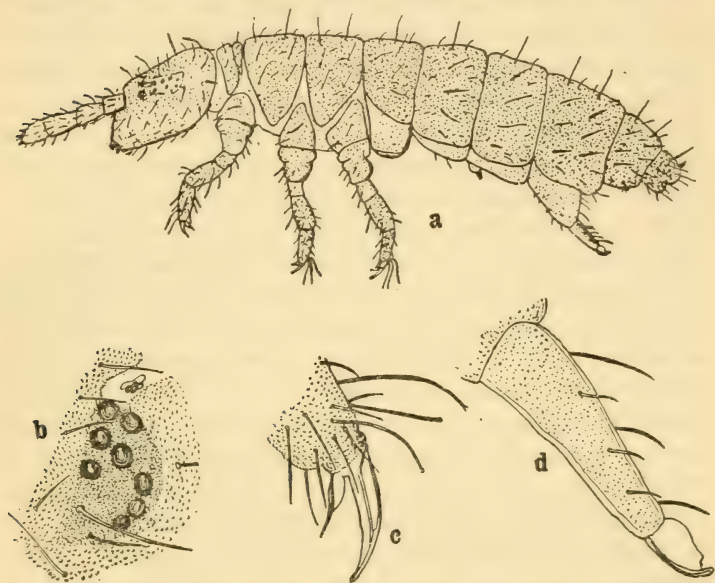


FIG. 66.—*a*, Springtail *Achorutes viaticus*, side view,  $\times 36$ ; *b*, right group of ocelli and post-antennal organ,  $\times 240$ ; *c*, hind foot,  $\times 300$ ; *d*, dens and mucro of spring,  $\times 240$ .

such occurrences, which have naturally attracted the attention of those responsible for the public health, may be explained by the sweeping in of colonies of the springtail in times of flood from waterside haunts in the catchment area of the town's supply. *Achorutes viaticus* is often common on the sea-shore, sometimes below high-water mark; the little insects crowd around the rich food-store in a putrid starfish. Similarly in most European

countries it is known to abound, and naturalists collecting insects in the far north find it common on the coasts of Spitsbergen, in Novaya Zemlya and in Greenland. Probably it inhabits all the continents of the globe, as it has been recorded from Tierra del Fuego, from New Zealand, and from small, sub-antarctic islands to the southward. Many other species of *Achorutes* have a known range nearly as wide as this, while a closely allied genus (*Gomphiocephalus*) and an obscure *Isotomine* springtail are the only non-parasitic insects as yet discovered by explorers of the great Antarctic Continent. G. Taylor has described (1914) how at Granite Harbour in South Victoria Land *Gomphiocephalus* swarmed on the surface of a small pool or clustered in a film of ice: "as one turned a pebble to the sun they would thaw out and crawl around for exercise." Delicate white and blind springtails (*Onychiurus*) are among the commonest members of our "soil fauna," often congregating in hundreds on soft plant tissues and decaying vegetable matter. One of this group—*Onychiurus armatus*—has nearly as wide a range as the *Achorutes* just mentioned, and is among those insects recorded by E. Handschin (1924) as present in the Swiss Alps to a height approaching 10,000 feet. Several species of springtail have long been known to disport themselves on the surface of the high Alpine snow-fields where masses of darker coloured *Achorutes* may appear as blackish patches conspicuous on the pure white background. And while such members of the order live far up the mountain heights, a considerable number of the springtails form a relatively large section of the fauna of deep caves. Among the white species mentioned above as living in the soil, is *Onychiurus inermis*; this insect is found commonly in the deep galleries of caves excavated in the Carboniferous Limestone districts of Great Britain and Ireland. All the species of *Onychiurus* are eyeless, and most of the springtails inhabiting caves are white and blind, even if they belong to groups whose members are normally provided with eyes. While some of the British and European cave springtails—such as *Heteromurus margini-*

*tatus*—are not known to live anywhere except in cave galleries, others like *Pseudosinella cavernarum* and *Arrhopaltes caecus* are found also in less profound dark dwelling-places, such as ants' nests, moles' nests, and quarry-tunnels or under large, deeply imbedded boulders.

These distributional facts about springtails have been mentioned in order to emphasise the exceedingly wide range of these frail, lowly insects, whether one considers the order as a whole or many of its component species. If we pass on to inquire the reason of this remarkable adaptability to surroundings often apparently so diverse, the answer seems to be furnished by the small size and comparative simplicity of form and function in these insects, which enable them to survive, increase, and multiply in haunts all of which afford a sufficient degree of shelter and an adequate and easily obtained food-supply, while the conditions as regards humidity allow the necessary gaseous exchanges to go on through the delicate body-wall. Springtails have undergone profound racial changes which may be regarded as indicating degenerative specialisation. Among these is the loss—total or extensive—of the typical insectan system of air-tubes for breathing ; these insects have reverted to a primitive method of breathing through the general surface of the skin such as is practised by the earthworms and other lowly organisms.

Another degenerative change is the disappearance of the compound eyes ; throughout the order these are replaced by sets of simple eyes (ocelli) eight at most on either side of the head (Fig. 66, *b*), and in many species there are no eyes of any kind. Such blind springtails have been mentioned as characteristic denizens of caves. They have often been regarded as blind on account of their residence in darkness through a long succession of generations ; but, on the other hand, caves and other similar dark places furnish haunts which are tolerated by creatures that cannot see, while those with well-formed eyes generally have the reaction of approaching any perceived source of light and will not therefore remain in darkness if, after wandering or being transported thither, they find themselves free to make a way



to the outer world. Those students of life-relations who doubt that such insects are blind because they dwell in caves might be willing rather to believe that they are found in such haunts because they are blind.

Though seeing little or nothing, springtails are, however, often provided with organs for receiving other kinds of sense-impression. Their bodies are frequently clothed with long tactile bristles; the impression conveyed by means of these must be of value in guiding the steps of insects living in darkness and obscurity. On the feelers are peg-like or bladder-like organs probably adapted to receive chemical stimulation and to guide the creatures in the search for food. On either side of the head, between the eyes and the base of the feeler, there is found in many springtails a problematical "post-antennal" organ consisting of a set of delicate areas or processes of cuticle, often arranged in form of a circle, an ellipse, or a rosette. To this goes a branch of the optic nerve, the fibres whereof may receive through it impulses due to vibration or chemical stimulation (Fig. 70, *b*).

Springtails as a group are very small, and their body-structure is remarkable among insects, because the number of abdominal segments is reduced from the usual ten or eleven to six. This contraction and shrinkage brings about a decrease in size which enables the insects to subsist on a relatively small food-supply; hence they can survive and propagate their race in apparently unpromising underground, arctic and alpine haunts where larger and more elaborately organised insects would speedily perish. They are able to hold their own under conditions which would be fatal to the large, strongly built and dominant butterflies and dragon-flies that we were previously considering as occupiers of wide territory.

It is now time to turn to examples of insects adapted to special kinds of environments, and the first feature for discussion in this connection is the general form of the creature. An insect's body is made up of a number of segments, arranged in series, one behind the other, and the

width of each segment seen in end view is often greater than its depth, the ventral surface of the cuticle is, as a rule, markedly convex, while the dorsal aspect is less convex or flattened. Such a body-form is seen in earwigs, cockroaches and the great majority of beetles, which are adapted for life on the ground and move principally by walking or running. A relatively broad body is clearly best adapted for this mode of progression; the same general form is also seen in many insects of comparatively feeble flight. In insects of large size which live under stones or among leaves, the dorso-ventral flattening is carried so far that the body becomes very much wider than deep. This is apparent in most cockroaches which live in the warm countries where they abound in forests among fallen leaves or under bark. In the familiar cockroaches which have been introduced into our cooler regions, we notice that this flattened form enables them to creep into warm shelters between the bricks of stove or oven settings, and behind or beneath hot-water pipes. In another household insect—smaller and more unpleasant than the cockroaches—the blood-sucking “Bed-bug,” the flattening is carried to an extreme so great that the breadth of the abdomen is twelve times as great as its depth and the upper surface becomes concave. Here we see a form of body suited to a creature that lives as a parasite closely adjacent to the skin surface of its host, and finds shelter in the crevices of wooden furniture (Fig. 67, *a*, *b*). It is suggestive, however, to remember that among insects of the order (Hemiptera) to which the Bed-bug belongs, a flattening of the body, similar if less extreme, is a common feature.

Among insects that are pre-eminently aerial in their mode of life we notice an increase in the depth of the body in proportion to its width. This is often particularly evident in the thorax, where provision has to be made for space and attachment for the powerful flight muscles, but a deepening and relative narrowing of the abdomen may often be noted. In many Hymenoptera and Diptera the abdominal segments are distinctly broader than deep, but

in ants, and bees, and wasps the vertical dimension of the abdomen approaches, equals, or exceeds the horizontal, as it does among the more highly organised members of the various groups of two-winged flies—gnats, midges, and the house-fly group. Similar proportions characterise most of the Lepidoptera (moths and butterflies). In dragon-flies also the body is, as a rule, deeper than broad; these insects have elongate abdomens which being narrow offer little resistance to the air in swift flight; it is interesting to

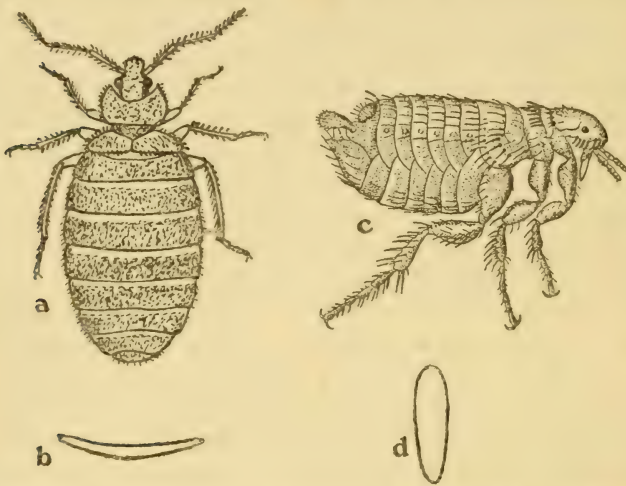


FIG. 67.—*a*, Bed-bug (*Cimex lectularius*), dorsal view,  $\times 5$ ; *b*, diagrammatic cross-section of *Cimex* to show dorso-ventral flattening; *c*, Dog-flea (*Ctenocephalus canis*), lateral view,  $\times 12$  (from L. O. Howard); *d*, diagrammatic cross-section of Flea to show lateral flattening.

remember that their grubs crawling on the bottom of pools and streams have bodies often distinctly broader than deep.

In contrast to the flattened cockroaches, the grasshoppers and locusts, belonging to the same order (Orthoptera) as they, have bodies distinctly deeper than broad. These insects are often strong fliers, and instead of running along the ground, they spend much of their time crawling on the stems and leaves of plants, whence by the action of their



long and powerful hind-legs, they leap into the air, not alighting again until a great distance has been cleared. The compression of the body that characterises them is clearly suited to their movement by great vertical jumps. It is interesting to notice the same modification of form carried to an extreme degree in those well-known parasites the fleas—wingless but obviously related to winged insects—whose bodies are so compressed as to be three times as deep as broad (Fig. 67, *c*, *d*). They also are active vertical leapers, their agility affording them the chance of getting on to fresh hosts, and in this respect they afford a most interesting because independent parallel to the grasshoppers, and a striking contrast to the bugs, which are like themselves parasites.

A form of body cylindrical or approximately so, is familiar in many insect larvae such as caterpillars and maggots. In a caterpillar (Fig. 45) this shape together with the support afforded by legs and pro-legs all along the body-length is well-suited for crawling and feeding along twigs or leaf-edges, as well as on leaf-surfaces. Among maggots and grubs generally the rounded form of body, whether cylindrical or tapering, is adapted for burrowing in the plant tissues or refuse which furnish the food supply of so many insect larvae of diverse orders. Among adult insects the cylindrical body is especially characteristic of wood-borers. The well-known "shot-hole" borings in old furniture and timber roofs indicate the presence of Ptinids ("death-watch") beetles which live in tunnels excavated in the wood and feed on the material thus bitten away. These beetles are all approximately cylindrical in body form, and a similar shape is noticeable in beetles of other families which practise the same manner of life. Of these the Bostrychidae are akin to the Ptinidae, but the Scolytidae, or bark-beetles (Fig. 49), like those in general aspect, are distinguished by many important structural characters, and belong to a distinct group of the order. We notice here again, therefore, independent and parallel modification of form in two or three different families in

correspondence with their dwelling-places and with the conditions of their lives.

The adaptation of many insects to their haunts, in such a manner that they resemble in appearance, to a greater or less extent, the objects among which they live, offers a subject of great interest. Examples have been, however, frequently described and discussed, and some contribution to the question will be attempted in a later chapter (XII), when the fascinating problems of insect evolution generally will be considered. For the present, therefore, it may suffice to recall a few cases illustrative of these relations between insects and their surroundings. Caterpillars feeding on leaves are frequently green in colour because the pigment of the plant tissues within the food canals passes into the fat-body and becomes apparent through the translucent skin and cuticle. But dark pigment may be developed in the skin, and as this happens to an increasing degree, the caterpillar tends to become darker and may approximate in appearance to the brownish bark of the twigs of its food plant or the dark soil. E. B. Poulton (1890) and others have shown that the appearance of the caterpillars is a response to the nature of the light reflected from their surroundings. If these be predominantly green, the reflected yellow rays penetrating the skin of the caterpillar, inhibit the development of the dark pigment, so that the insect appears green, because that colour shows through the body-wall from material in the deeper tissues. It is found, therefore, that many caterpillars are notably variable as to colour, appearing dark or green according to the predominant colour of their haunts or food-plants. Thus they are endowed with what is termed "protective resemblance," because it seems likely that their appearance serves to hide them, so that they escape the observation of possible enemies which would devour them were they detected. Protective resemblance becomes more marked in cases where the insect is of such form that it resembles a twig of its food plant; this condition is well known in many of our "looper" caterpillars (Plate X) and in the "stick

PLATE X



CATERpillars of *Odontopera bidentata* ON TWIGs.

[J. P. Ward, photo.]



EMPTY CUTICLE OF STONEFLY NYMPH (*Perla*), after emergence of Fly.  
To face p. 272 ]

[H. Britten, photo.]





insects" (Plate I, A) of the tropics, while the Oriental "leaf-insects" have the wings as well as the flattened legs and abdomen shaped, marked, and coloured so as to resemble closely green or withered leaves. The wing patterns of many moths and butterflies are apparently of a nature to afford them protection by concealment when at rest on such objects as tree-bark, reeds, flower-heads, or lichens. The wonderful harmony of the upper forewing surface of the common moth *Agriopsis aprilina* with the greenish-grey lichens on the tree-trunks where it habitually rests has often been given as a perfect example of this particular type of adaptation to haunts shown by many insects. It is well known that most moths rest with the upper surface of the forewings in full view concealing the hindwings beneath, and that in many groups while the forewings are mottled brown or grey, these hindwings are brilliantly coloured—red or blue in *Catocala*, yellow in *Triphaena*. A similar adaptation in resting posture for concealment is shown by many of the grasshoppers and locusts of southern Europe and the tropics, the bright red or blue hindwings being folded and hidden beneath the inconspicuous brown or grey forewings.

When considering the manner in which insects are fitted to the places where they live it is of especial interest to turn to those that spend all or most of their time in water, because insects are essentially aerial creatures, with their air-tube systems for breathing strikingly adapted to the open atmosphere, as we saw in an early physiological discussion in this book (pp. 40-42), and yet we find among them, whether in the adult or larval stages of many families and orders, the most varied and beautiful modifications for aquatic life. In the course of the racial history of insects, water seems to have attracted them again and again from the early days of their presence on the earth.

The well-known book by L. C. Miall (1895) on *Aquatic Insects* serves as an excellent guide to a fascinating line of study for British workers at natural history. Many aquatic insects spend nearly all their lives in ponds and streams

either resting or moving about on the surface film, or diving and swimming through the water. The whirligig beetles (*Gyrinus*) may be seen darting or circling rapidly over the surface; they are then on the water but entirely in the atmosphere, for they depress without breaking the surface-film. A beetle thus skimming will then dive suddenly and cleave the water with rapid strokes of its oar-like middle- and hind-legs, carrying with it, between the extremity of its closed wing-covers (elytra) and the tail-end of its body, a bubble of air, the boundary of which gleams like a sphere of silver. This tiny enclosure from the upper atmosphere, in contact with the beetle's spiracles, enables it to continue breathing normally for a considerable time although submerged. The larva of *Gyrinus*, an elongate firm-coated grub with well-developed legs, has a series of paired thread-like hollow abdominal appendages which serve as gills for ensuring gaseous exchange between the cavity of its closed air-tube system and the air dissolved in the water. The *Gyrinus* grub is thus so specially adapted for aquatic life that it could not survive out of the water. Yet at the close of the larval period it crawls up the shoot of an aquatic plant and spins a silken cocoon between the leaves; within this it pupates and the pupa with its paired series of open spiracles breathes atmospheric air in the manner usual with insects. Into the air therefore the beetle, when developed, must emerge, though, as we have seen, it spends most of its life on or beneath the surface of the water. Its possession of functional wings ensures the power of migration in case of need.

*Gyrinus*, like its much larger and well-known relation *Dyticus*, is a creature of prey. Another group of aquatic beetles with very different modifications for their special mode of life are the species of *Donacia* and allied genera belonging to the family of the leaf-beetles (*Chrysomelidae*) and vegetarian in their habits. While *Gyrinus* and *Dyticus* have smooth boat-like contours to the body and the hinder legs broadened like paddles, the *Donaciine* beetles are of an aspect like that of many members of their order which never



go near water, elongate insects of graceful form with slender unmodified legs. The species of *Donacia* are found crawling on the leaves of water-lilies, pondweed, sedges, or other aquatic plants; sometimes they go down into the water for brief periods, but their larger relations of the genus *Haemonia* are said to spend most or all of their lives submerged though no special arrangement for carrying down air has been detected in their structure. The egg-



FIG. 68.—*a*, Newly hatched larva of *Donacia palmata*,  $\times 50$ ; *b*, full-grown larva partly buried and feeding in stem of water-lily; *c*, the same breathing with tail-spine embedded in water-lily stem,  $\times 3$ . After A. D. Macgillivray (N.Y. State Mus. Bull. 68, 1903).

laying habits of these beetles have been described in some detail by A. D. Macgillivray (1903) and A. G. Böving (1910). The female, living on the surface of a floating water-lily leaf, often eats out round holes penetrating to the lower leaf-surface and then thrusting the tip of her abdomen through, places her eggs in rows so as to form a circular or chordal area surrounding the hole; such is the habit of the European *Donacia crassipes* and the North

American *D. palmata*, the larvae of which descend to the bottom and feed on the underground stems and roots of the water-lily (Fig. 68). The eggs of other species are laid

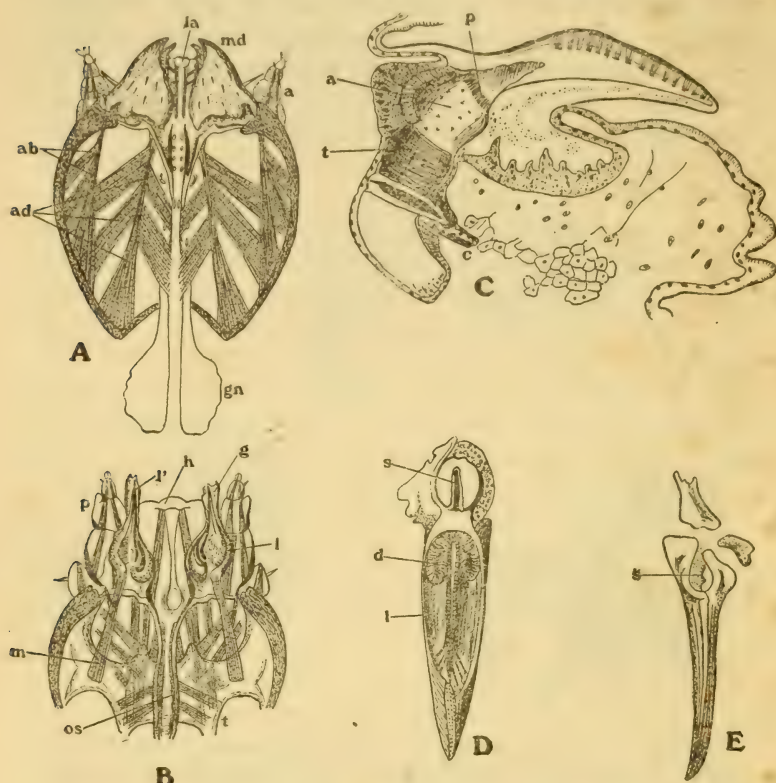


FIG. 69.—Structural details of larva of *Donacia*. A, head dissected from below: *a*, feeler; *md*, mandible; *ab*, *ad*, its abductor and adductor muscles; *la*, labrum; *gn*, subesophageal ganglion,  $\times 70$ . B, Front of head dissected from above: *p*, palp of maxilla; *g*, galea; *l*, base, and *l'*, point of lacinia; *m*, lacinial muscle; *h*, hypopharynx; *os*, gullet,  $\times 70$ . C, longitudinal section through tail-spine and adjacent region of abdomen; *t*, trachea; *c*, closing lever; *a*, atrium; *p*, passage to canals,  $\times 100$ ; D, tail-spine in longitudinal horizontal section. E, dorsal view: *s*, spiracular slit; *d*, dorsal, and *l*, lateral canals,  $\times 100$ . After A. G. Böving (*Int. Rev. Hydrobiol.* 1910).

in masses or singly on various aquatic plants whence the newly hatched grubs make their way downwards into the

water to feed between leaves or on stems. The larvae of *Haemonia* feed on *Potamogeton*.

The grubs of these beetles are soft-coated and thick in the middle of the abdomen, tapering towards the head and tail ends ; on the thorax are three pairs of short jointed legs. So far the grub resembles many of the vast host of leaf-beetle larvae that feed on land plants, but the stout biting mandibles have no grinding area. The maxillae are remarkable in having the inner lobe (lacinia) modified into a strong piercer (Fig. 69, B, I) partly sheathed by the delicate sub-tubular outer lobe (galea). When the grubs are feeding, not the head only but the greater part of the thorax also, is imbedded in the plant-tissue. From his examination of the jaws and the contents of the food-canal, Böving concludes that these grubs bite the plants in order to obtain and suck sap ; they do not swallow solid pieces of tissue.

Living submerged for several months, probably more than a year, the Donaciine larvae require some provision for breathing. It is well known that the great majority of aquatic insect grubs breathe in one of two ways. Many of them get continual or intermittent contact with the upper atmosphere, usually by thrusting through the surface film an outgrowth or processes at the tail-end of the body, directly continuous with the spiracular and air-tube system as in the case of the gnat-larva (*Culex*) and the rat-tailed maggot of the drone-fly (*Eristalis*), or affording a channel by means of which air can reach the protected spiracles as in the case of the large carnivorous water-beetles (*Dyticus*) and the water-scorpion (*Nepa*). Many others make use of the air dissolved in the water by means of various types of tracheal gills, like those of the slender dragon-flies (*Agrionidae* or damsel-flies) and the mayflies ; or blood-gills like those of the caddis-larvae and the grubs of midges belonging to various families of *Diptera*.

The adaptation of the Donaciine larvae is especially remarkable because they make use of atmospheric air which they seek not above the surface-film but enclosed in the tissues of submerged water-plants. It has been mentioned



how these grubs feed by burying the head and thorax in the stems or root-stocks of water-lilies and other aquatic vegetation. They may also be seen with tail-region fixed to water-lily stems or the roots of water *Ranunculus*, and in this position they are breathing. Attachment of the grub to the plant-shoot is made by a pair of strong, slightly curved, pointed structures which project backwards from the dorsal aspect of the eighth abdominal segment over the tail-end of the larva. These spines serve to pierce the submerged plant-tissues and penetrate to the internal air-spaces. Each spine is ovoid in cross-section, has ventrally a thick chitinous wall, and is hollow, containing two large lateral canals separated by a median partition, and also smaller dorsal canals. The arrangement (Fig. 69, C, D, E) has been studied by MacGillivray, in greater detail by Böving. The lateral canals pass into a relatively spacious chamber (atrium) at the base of the spines close to the front edge of the eighth abdominal segment; into this chamber open the dorsally situated spiracles and the tracheal trunks. The hollow spines penetrating the air-spaces in the plants, open a way by which air can pass into the grub's tracheal system, and the spiracular passage can be opened or closed by suitably arranged muscles. A curiously normal feature of this grub, submerged through its whole life, is that it possesses the pair of thoracic and the seven other pairs of abdominal spiracles usually found in insect larvae that live in the upper air. It appears that these spiracles, exposed on the surface of the cuticle, are indeed functional, but only for the expiratory phase of the creature's breathing. Thus it takes in air from the plant tissues pierced by its spiracular spines and breathes out through the series of small paired spiracles along the main length of its body which is always surrounded by water. "That the *Donacia* larva," as Miall has well remarked, "should have found out the air-reservoirs of submerged roots, and possess special organs for tapping them, is surely one of the curiosities of adaptation."

The pupae of the *Donaciine* beetles are found in closely

woven cocoons, attached to the water-plants where they fed and breathed as larvae, and although the adult beetles emerge from the pupal cuticle in autumn, they remain in their submerged cocoons through the winter. The dense wall of the cocoon, water-tight and air-tight, is formed largely of silk derived from modified salivary glands, and partly, according to Böving, of the secretion of skin-glands with the addition of the ejected and hardened contents of the food-canal. MacGillivray states that the larva works at its cocoon with the spiracular spines embedded in the plant-tissues from whose air-spaces the cocoon becomes inflated with air when complete. Then the larva withdraws from the plant stem or root and turns round before casting its cuticle. Through the scar in the stem or root abundant air-supply can pass from the air-spaces to provide for the breathing of pupa and beetle until the spring season arrives when it emerges into the upper air. The ventral surface of the body being covered with fine hairs, a water-film surrounds it, so that the beetle has an air-bubble over the spiracles as it rises at last into the atmosphere, after its prolonged immature existence under water. It has already been mentioned that some of these insects may descend again beneath the surface-film in order to feed and lay their eggs on the submerged aquatic plants.

The short hairy clothing of the Donaciine beetles affords an example of a condition common in many aquatic insects for enabling them to crawl or dive under water without the actual surface of the cuticle and its open spiracles becoming wet. The tips of such hairs are too close together to allow water to penetrate between them; as the insects pass beneath the surface the film on which they press remains unbroken, and when the insect is submerged a layer of air, evident from its silvery sheen, extends over at least a portion of its body; thus it takes with it into the water enough of the atmosphere to supply for a while its needed oxygen. The tension of the surface-film of water, well known to students of physics, renders possible some of the most remarkable adaptations of aquatic insects;

this point is admirably elucidated in Miall's well-known book (1895). He points out how in the common gnats (*Culicidae*) the surface tension has a part to play in every stage of the life-history. The eggs are laid on the water—over two hundred glued together to form the familiar “raft.” Each egg is elongate, broad at one end with a circular outline, narrow at the other; the narrow pointed ends are so close together that the water cannot get between them; therefore, as they are always separated by air-spaces, they must remain upwards as the raft floats, and the submerged end of each egg opens by a round lid to allow the newly hatched larva to dive into the water. The larva has in connection with its hindmost spiracles, which alone are functional, a prominent tube diverging from the tail-end of the body; the opening of this tube is surrounded by a set of pointed flaps which close it when brought together. The larva, rising tail-first to the surface, pierces the film with the adjacent points of these flaps, and then separates them so that they form at the surface a cup-like depression leading into the spiracle tube. Areas of film are held between adjacent edges of the flaps, so that the gnat grub hangs as it were from the surface supported by the tension of the film which is pulled downwards by the drag of the larva, but not broken. When the spiracular valve is closed by the drawing together of its pointed flaps, the tips of the processes can be disengaged from the surface and the larva dives, its air-tube system completely shut off from the surrounding water. (See Fig. 87, *b*.)

The restriction of the gnat grub's functional spiracles to the hinder end of its body enables it—like many other larvae of *Diptera*—to breathe at its tail while it feeds with its mouth. The gnat pupa, on the other hand, has a pair of respiratory trumpets on the prothorax projecting dorsally. By means of these it can hang and breathe from the surface-film, the strongly arched dorsal region of its thorax uppermost and its abdomen pointing downwards. This attitude is in preparation for the emergence of the gnat into the atmosphere, for the pupal cuticle slits length-



wise along the dorsal axis of the thorax, and through the slit of the body, head, feelers, jaws, legs of the developed insect are all withdrawn upwards. The empty pupal cuticle may float at the surface, serving as a raft whereon the gnat may rest and let her wings spread and harden.

The surface tension of a sheet of water not only enables such submerged larvae and pupae to breathe atmospheric air ; it also allows a large majority of insects to live and move freely over the surface without getting wet. A quiet pool or the calmer reaches of a stream often bear on a summer day numbers of insects, gliding, skating, or even leaping on the surface-film. Among these the slender, active, long-legged flies of the family Dolichopodidae are often conspicuous ; they stand in readiness on the water and dart across the surface to catch suitable prey. Springtails of several distinct groups which live in large assemblages on the surface of water—*Podura aquatica*, for example—often fall victims to these flies. But the surface-living habit is especially well developed among the Hydrometridae, a family of Hemiptera, insects with sucking and piercing mouth-parts which pass through no marked transformation in their life-history. Most of these aquatic bugs are slender and elongate in form. *Hydrometra stagnorum*, with its long, narrow head and body and stiff thread-like legs, is wonderfully adapted for life on the surface-film which supports it without showing any appreciable depression. The true pond-skaters belonging to the genus *Gerris*, of which there are several common British species, are less slender in body than *Hydrometra*, but their middle and hind-legs, which spread far out on the surface, are straight, thin, and rigid except at the joints. The short, two-segmented feet bear on the surface-film, which they depress to such an extent that they make, as Miall remarks, “ little dimples on the water,” which are apparent when the sun is shining on one of these insects standing in a shallow pool, as then “ the dimples cast shadows on the bottom, each surrounded by a bright ring due to refraction of the rays which pass through the curved surface.” The fact that

no such light region surrounds the shadow of the body shows that the legs keep it raised above the surface. While in *Hydrometra* all the legs are elongate and slender, in *Gerris* the foremost pair are relatively short and robust, the feet provided with strong hook-like claws springing from a cleft in the terminal foot-segment. By means of these the pond-skater can anchor itself to floating objects, such as the dead insects whose juices it sucks for food. The middle legs of *Gerris* and its allies are inserted far back owing to the ventral and lateral extension of the mesothorax ; thus the limbs are placed close to the hindmost pair, and when the insects glide over the surface all four, with long, sweeping strokes, move in unison. A related form, *Velia currens*, common on swift streams, is more robust in build than *Gerris* with less specialised legs. It obtains, however, good support through the surface tension and occasionally dives and swims under water. It makes use of the tension from below, for Miall remarks that " it can be seen to run, back downwards on the surface-film, completely immersed in the water ; its abdomen at such times glistens with the air-bubble which overspreads it." The short hairy clothing of the cuticle to which the formation of such a bubble is due is especially dense in many of the aquatic Hemiptera.

An interesting modification shown by many of these insects is a partial suppression of the wings. In some species of *Gerris* the wings may be absent in the adult, or present only in a reduced condition, while in other individuals of the same kind wings are fully developed. Most adults of *Velia currens* are wingless, but winged specimens are occasionally found, and such must form a fairly numerous minority of the whole population of the species. The disappearance of wings is not surprising among insects which cling through most of their lives to the surface of freshwater pools and streams ; but as many of their haunts are liable to dry up, the occasional development of winged members capable of flying away to fresh watery feeding-places is clearly advantageous to survival.

From consideration of some of the great multitude of

freshwater insects it is natural to turn to a few examples of the comparatively small number—probably, however, amounting to hundreds of species—that haunt the margins and tidal waters of the sea or venture themselves on its surface. Insects are pre-eminently creatures of the air and the land; therefore we are surprised to notice the wonderful modifications shown by many of them for life in water, and the adaptation of others to marine conditions is yet more surprising. Many of the marine insects, such as aquatic beetles and bugs, and flies with submerged larvae, with their near allies among freshwater groups, have passed to sea through the brackish waters of estuaries or salt-marshes. Others, belonging to groups that feed whether as adults or larvae in decaying organic matter, seem to have been attracted by the row of blackened seaweed that marks the high-tide level along the coasts; thence some have passed on to find shelter and food in the varied animal and vegetable substances along the tidal belt. Attention has already been drawn in this chapter (p. 267) to the adaptability of the *Collembola* (springtails) to very widely separated and diverse haunts, largely owing to the comparative simplicity of their structure. There are a number of springtails of the *Isotomine* group to be found among the decaying wrack flung up by the waves. Some of these belong to species that live also inland, but some are known only from the tidal margin though in widely separated parts of the world. For example, *Archisotoma beselsi* (Fig. 70), a characteristic member of the fauna of Spitsbergen, lives along the high-tide mark of our British and Irish coasts as well as in similar situations in Greenland, Tierra del Fuego, and the sub-antarctic South Orkneys. Often very abundant where found, this little insect appears to inhabit only the tidal margins of the sea-coast in widely separated regions of the globe. The most characteristic of shore-haunting springtails is *Amurida maritima*, found in vast numbers along the rocky coasts of our islands, of France, Heligoland, and North America. Its form and habits have been described in detail by A. D. Imms (1906). It is one of



those Collembola in which the spring is absent in the adult, though the rudiments of that organ appear in the embryo, and remain as vestiges in the newly hatched young. The cuticle of Anurida is covered with minute tubercles which

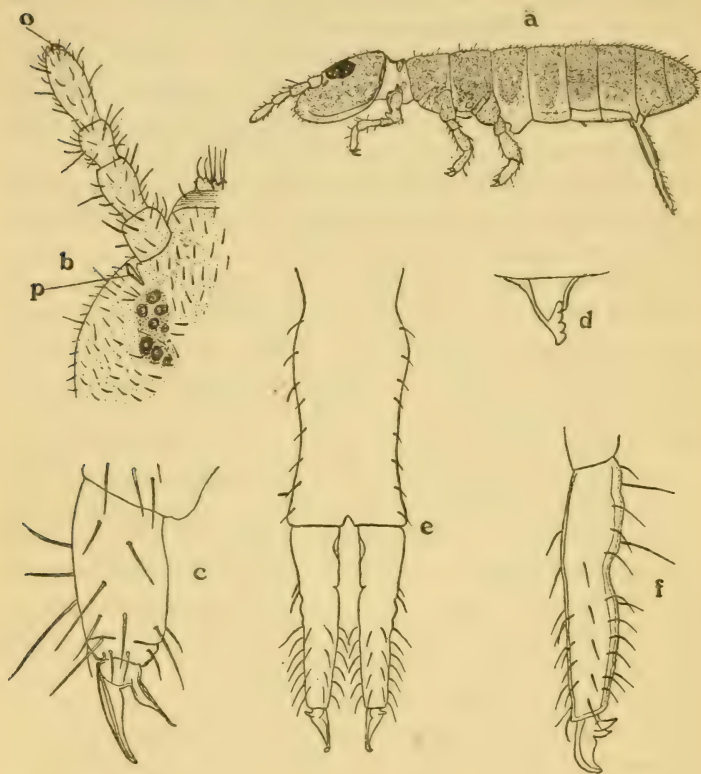


FIG. 70.—*a*, Seashore Springtail (*Archiostoma beselsi*), side view,  $\times 30$ ; *b*, left frontal region, showing feeler with terminal sense-organ, *o*, post-antennal organ, *p*, at its base, eight ocelli behind,  $\times 90$ ; *c*, shin and foot of hind leg,  $\times 240$ ; *d*, catch; *e*, spring (dorsal view),  $\times 150$ ; *f*, dens and mucro of spring (lateral view),  $\times 240$ .

support the film surrounding an air-bubble which encloses the insect when submerged. Anurida is found only between tide-marks where it shelters in cracks of the rocks, among seaweeds, or in the empty shells of molluscs. When, as

often happens, a large assemblage of Anurida collects on the surface of a rock-pool, the little creatures become conspicuous at low water to a keen observer. The mass of blackish springtails may be blown across the surface by the wind, and some members of the crowd climb on to the backs of others or do their best to clamber up the rocks among the crevices and vegetation in which they appear to find their normal homes and feeding-grounds.

The Beetles (Coleoptera) are represented among marine

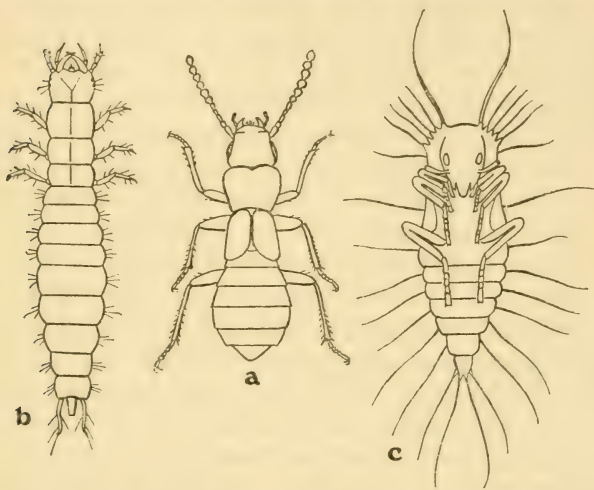


FIG. 71.—*a*, Seashore Rove-beetle (*Micralymma brevipenne*), Western Europe,  $\times 10$ ; *b*, larva; *c*, pupa (ventral view),  $\times 12$ . After Laboulbène (*Ann. Soc. Ent. Fr.* (3) vi, 1858).

insects by a number of species belonging to several distinct families. The zone of decaying seaweed at high-water mark is the haunt of various rove-beetles (Staphylinidae) which, with their grubs, feed on the fly-maggots that eat the soft "wrack." Some members of this family live between tide-marks; the broad-bodied *Micralymma brevipenne* (Fig. 71), with its reduced wings, may be found lurking in rock-crevices or walking over shingle exposed at the ebb. This species preys on the springtails (Anurida) whose haunts it has invaded. Both its larva and its pupa (Fig. 71, *b*, *c*)

are furnished with a remarkable hairy covering which probably assists them to secure air-bubbles for breathing when submerged. The leaf-beetles of the Donaciine group, whose adaptations for aquatic life have been described, have a species, *Haemonia curtisi*, which lives always in brackish water, feeding on the Sea-wrack (*Zostera*) and breathing in the same way as its relations do on the water-lilies and other plants of ponds and streams. Some of the marine ground-beetles (Carabidae) are of especial interest. All beetle-collectors know many species of *Bembidium*, usually small dark beetles that lurk in damp places, several haunting the sea-shore above high-water mark. *Cillemus lateralis* is an allied form, wingless with bronzy green head and thorax and sandy wing-cases found on the sand or among stones between tide-marks from the British and Dutch coasts southwards to North Africa. They run in the sunshine on the expanse left by the ebbing tide; when the water comes in they seek shelter under stones or burrow in the sand. They have relatively powerful and sharp mandibles and prey on the sandhopper *Talitrus*, as A. H. Haliday observed ninety years ago (1837), "seizing them by the soft part of the under side, and in this way are able to master game many times their own bulk. Sometimes three or four beetles may be found in concert attacking a sandhopper of the largest size. The tide returning has scarcely uncovered the sand when these little depredators are abroad from their hiding-places and alert in the chase." But the tiny beetles of the genus *Aepus* only 2 mm. ( $\frac{1}{12}$  in.) long are perhaps the most remarkable marine insects of the whole order; they may be recognised by the relatively enormous head, the broad truncated abdomen and the short wing-cases, wings being quite absent. Our two British and Irish species, *A. marinus* and *A. robini*, range south to Spain and out to the Madeiras. The widened fore-shin has a comb-bearing notch for cleaning the feelers from grains of sand. The long, bristly hairs serve to entangle air-bubbles when the beetles are submerged, as was first noticed by J. V. Audouin (1833). "If," he wrote, "one



transfers the insect directly from air into sea-water, one notices that each of its hairs holds a little layer of the surface-film, forming at first tiny spheroids ; these soon unite into a little globule which surrounds its body on every side, and which, despite the agitation resulting from the insect running under the water, never escapes." The air-tube system of *Aepus* is furnished with two broadly ovate reservoirs in close connection with the hindmost pair of spiracles. These, as Miall remarks, "are no doubt useful during prolonged submersion." The compound eyes of *Aepus* are remarkable, the corneal facets being circular in form and few in number and protected by a chitinous plate perforated by a central round hole. Adults and grubs of *Aepus* are believed to prey on small molluscs such as *Rissoa*, in whose company they may often be seen.

The most conspicuous of all the sea-shore insects are certainly the Diptera or two-winged flies. Over the mass of seaweed thrown up by the waves at high-water mark run hundreds of small brownish or greyish flies—many of them related to the group of the house-fly and bluebottle. Their maggots feed on the decaying marine vegetation below. The maggot of *Fucomyia frigida*, described by E. V. Elwes (1915), has the tail-spiracles surrounded by delicately branched bristles, well adapted for holding air-bubbles. Though belonging to several distinct genera—*Fucellia*, *Coelopa*, *Orygma*, for example—most of the seashore flies have a characteristic general aspect which suggests adaptation to their strange haunts, a flattened form of body, angular head with small eyes, markedly spiny or hairy legs, and narrow wings. They run rapidly over the dark accumulation of wrack, frequently rising and flying for short distances ; their wings are not suited for prolonged flights. On the shores of the windswept sub-antarctic island of Kerguelen live flies of this group described by E. A. Eaton (1879) in which the reduction of the wings is carried still further ; *Anomalopteryx maritima*, with narrow strap-like wings, lives on the nests of seabirds, while *Apetenus litoralis* creeps over the stones of the beach. A. R. Wallace (1889)

and others have pointed out how many of the insects on oceanic islands are flightless, and suggested that this condition may be regarded as advantageous, as flying insects in such localities would be in continual danger of being blown out to sea. It is possible also that life close to the sea-shore of continental tracts and islands is safer for insects that fly infrequently or not at all. Returning to the flies of our own coasts, it is interesting to find among the predaceous Empidæ—a family belonging to a section of the Diptera far removed from *Coelopa* and its allies—the little sand-haunting *Chersodromia arenaria*, which shows the same small head and flattened body-form as these, and has its wings not only narrow and pointed but so shortened as to be useless for flight.

Perhaps the most characteristic and specialised of all shore-haunting Diptera are some minute midges of the family Chironomidæ, the adaptation of whose larvae for aquatic life has already been mentioned (p. 45). Chironomid larva have been dredged off the European and American coasts at depths of 15 and 20 fathoms, and one of these was described as a marine annelid by a naturalist who failed to recognise it as an insect grub. Several species of *Chironomus* and allied genera haunt the rocks exposed at low tide, and the more remarkable of these show the tendency of marine flies already mentioned towards loss of wings. In *Eretmoptera browni*, described by V. L. Kellogg (1900) from the coast of California, the wings in both sexes are “narrow and strap-like and wholly without veins, not specially thin or delicate but rather thickened.” A structural feature of much interest, suggesting the primitive standing of the insect, despite its adaptation for marine life, is that the hindwings instead of being the stalked, knob-like “balancers” usual among the Diptera, “are minute scale-like processes, appearing like rudiments of wings” of the ordinary type. “The flies,” remarks Kellogg, “of which there were very many, were resting and running on the surface of the ocean water of tide-pools and had a tendency to gather in large numbers in patches

and in ball-like masses on the water." On Kerguelen, Eaton found females of a tiny midge (*Halirytus amphibius*) with short feelers, slender legs, elongate body, and wings reduced to the smallest vestiges. These frail creatures live "at the verge of the tide, creeping over Enteromorpha and mussels exposed by the recess of the sea and walking on the surface of the puddles and tide-pools." Eaton observed the midges crowded "on small isolated rocks always submerged at high water," and suggests that when the receding tide leaves these rocks bare, "all the flies hurry up from below to take an airing."

A little midge, *Clunio marinus*, which haunts the tidal margins of the Irish, British, and French coasts, does not yield in interest to its relations in remote quarters of the globe. The male was described by A. H. Haliday (1858), who found numerous specimens in Kerry "on gravelly sea-coasts below high-water mark, walking with the wings half raised and in rapid vibration without taking flight." The wings, indeed, though relatively broad and well-proportioned, are short in comparison with the insect's somewhat massive abdomen, and serve as sails rather than organs of flight; the little midges with their elevated wings skim over the surface of the rock pools. A. D. Imms (1903), however, describing the habits of *C. bicolor* on the coast of the Isle of Man, states that the male flies "short distances at a time, generally about two feet," and that it skims over the water and rocks within a few inches of the surface. The thorax of the male (Fig. 72, *a*) is large and hood-like, protecting the retracted head with its small eyes, the cornea of each composed of few oval facets. The jaws are so reduced that the midges in the adult state can take no food and their lives must be very short. The female of *Clunio* was discovered and described independently by R. Chevrel and G. H. Carpenter (1894) on the French and Irish Channel coasts in *C. bicolor* and *C. marinus* respectively. She is a wingless and degraded insect, with elongate hind-body, short and feeble legs, a small head bearing feelers with few segments, and very reduced eyes (Fig. 72, *b*).



The assemblages of *Clunio* can be observed only during the low spring tides, when the rocks on which they live are exposed twice daily for a week or so. The males skim, as already mentioned, over the surface of the tidal pools; they also crawl on the masses of the bright green seaweed *Cladophora*, where the wingless females creep and on which the larvae feed. M. Bezzi (1913) has given an account of the four species of *Clunio* known from the Atlantic, Channel, and Mediterranean coasts. When pairing takes place, the male seizes his mate by means of his powerful claspers,

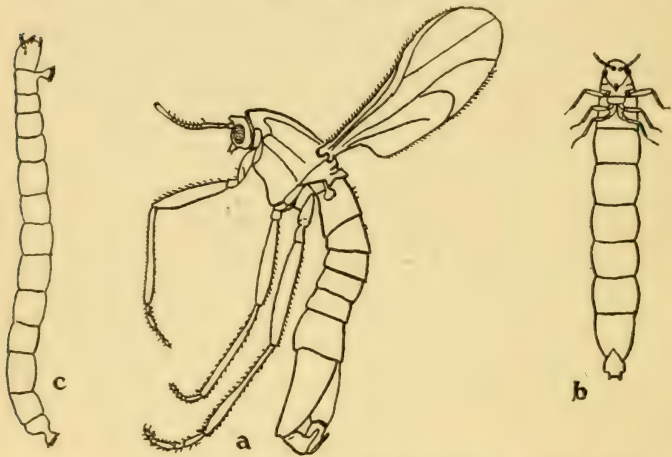


FIG. 72.—Chironomid Midge (*Clunio marinus*), British and Irish coasts. *a*, male (side view); *b*, female (ventral view); *c*, larva (side view),  $\times 20$ . After Carpenter (*Knowledge*, xxiv, 1901).

holding her so that her elongate body is in a line with his own, her feet clear of the surface whereon he walks, kicking in the air. After half an hour's promenade the male releases the female, who proceeds to lay her eggs, fifty to over a hundred in number, enclosed like those of *Chironomus* in a cylindrical gelatinous tube which is attached to rock or seaweed. Chevrel has given a picturesque account of the egg-laying process and its sequel. "When the operation is finished the female, exhausted by the efforts which she has made, can only move slowly, she walks painfully, stops

often, and only regains a little strength after resting for several minutes. Then she wanders at random, and ends by falling into the water, and floating on the surface, waits for death, which is never long delayed." He noticed that her feet often became caught in the gelatinous substance of her egg-tube ; then she fails to disengage herself and dies

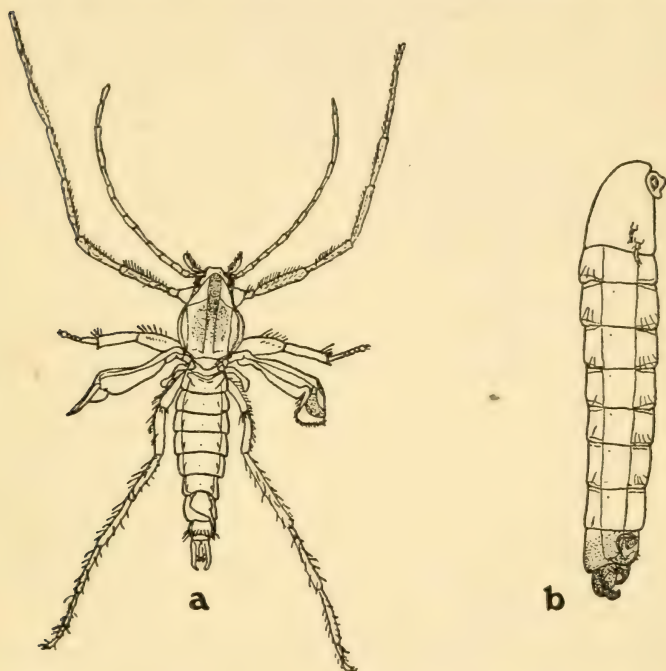


FIG. 73.—Submarine Midge (*Pontomyia natans*), Samoa. *a*, male (dorsal view); *b*, female (side view),  $\times 20$ . After F. W. Edwards (*Proc. Zool. Soc.* 1926).

resting on her eggs. The reduction of the jaws in these midges, so that they are incapable of feeding, prepares us to expect that they do not long survive the functions of pairing and egg-laying ; the week of low spring tides during which they are active, is enough for the perpetuation of the race. The eggs are hatched a week after laying, and the beautiful little green larvae feed on the *Cladophora* that

clothes the rocks. The grub (Fig. 72, *c*) has a brown head with obliquely set mandibles, and paired pro-legs with circles of hooklets on the first thoracic and last abdominal segments. In these characters it resembles closely the "bloodworm" larva of an ordinary freshwater Chironomus; but it needs no special blood-gills for respiration, breathing all over the surface of its delicate and transparent body-wall. Several shore-haunting Chironomidae from Samoa have been recently described by F. W. Edwards and P. A. Buxton (1926). These include a species of *Clunio*, and a new type (*Pontomyia natans*) which is perhaps the most remarkable of all marine Diptera. The male (Fig. 73) has very long fore and hind legs, the wings reduced and twisted, and the spiracles closed. This insect lives entirely submerged, swimming at night with its long legs and narrow wings and breathing through the delicate body-wall. During daylight the midges are believed to hide in the patches of *Halophila*, a pond-weed like plant that grows in the Samoan lagoons. The female *Pontomyia* (Fig. 73, *b*) is wingless like that of *Clunio*, but still more degenerate, as fore-legs are quite absent and the others reduced to tiny vestiges. Buxton believes that she spends her whole life in "the mud tubes among the leaves of the plant *Halophila*, where the larvae and pupae are also found. No other insect submarine in all its stages had been previously observed.

In our survey of examples of freshwater insects (pp. 281-282) reference was made to several members of the Hemiptera such as *Gerris* and *Velia*. These bugs have relations living on the sea-shore or on the surface of the estuaries and oceans, which are perhaps the most remarkable of all marine insects as regards adaptation to their special and unusual haunts. In some families a gradual transition from terrestrial to salt-water surroundings may be traced. The dull, ovate insects of the genus *Salda*, for example, have some species frequenting dry heaths, others haunting the edges of ponds and streams, others again living on salt marshes or close to tidal waters. These are well able to



endure submersion, creeping about under the salt water at high tide. Allied to the Saldidae is the remarkable *Aepophilus bonnairei*, regarded as the type of a distinct family, the only member of the order that lives between tide-marks on our coasts, where it is found in the same situations as the beetles *Aepus marinus* and *A. robinii*, already mentioned in this chapter; hence the name conferred on it by its discoverer V. Signoret (1880). It is an elongate, flattened hairy bug (Fig. 57), resembling the bed-bug in its vertical compression as well as in the absence of hind-wings and the vestigial, pad-like condition of the strong forewings. R. Koehler (1885) found these insects on the coast of Sark beneath large stones in a cave, entrance to which is only possible to human beings four times a year. J. H. Keys, whose observations on the family life of these bugs have been previously mentioned (p. 212), found the insects to occur in greatest numbers beneath large boulders in a channel far out beyond a reef of rocks, a locality covered by the sea for twenty hours of the twenty-four. They cannot apparently survive prolonged immersion in seawater, nor can they walk on the surface; "they hide in companies in little holes in the stone, packed together as closely as possible, or rest on the algaic growth thereon." In such shelters though submerged they are encased in air-sacs and not really immersed. *Aepophilus* is apparently a scarce insect with a range restricted to the coasts of south-western Europe, the Channel Islands, south-western England, and southern Ireland.

The most highly specialised and strongly adapted among marine Hemiptera belong to the family (Gerridae) of the pond-skaters and their allies. The common *Velia currens* of our streams (p. 282) has in the tropics relations known as *Rhagovelia*, in which the legs of the middle pair are exceptionally long and provided with a system of branching feathery hairs set in the deep cleft of the terminal segment of the foot. These can be retracted and hidden within the cleft of the foot or spread out like the spokes of a wheel to provide a disc-like area of support on the surface-film.

This wonderful and beautiful "wheel-foot" is characteristic of the allied *Trochopus* (Fig. 74, *c*, *d*), whose species, wingless and marine, skim over the surface of tropical American seas not far from land. They are covered with dense velvety hairs, and as a result carry down with them an air-bubble when they dive; this adaptation, common to a

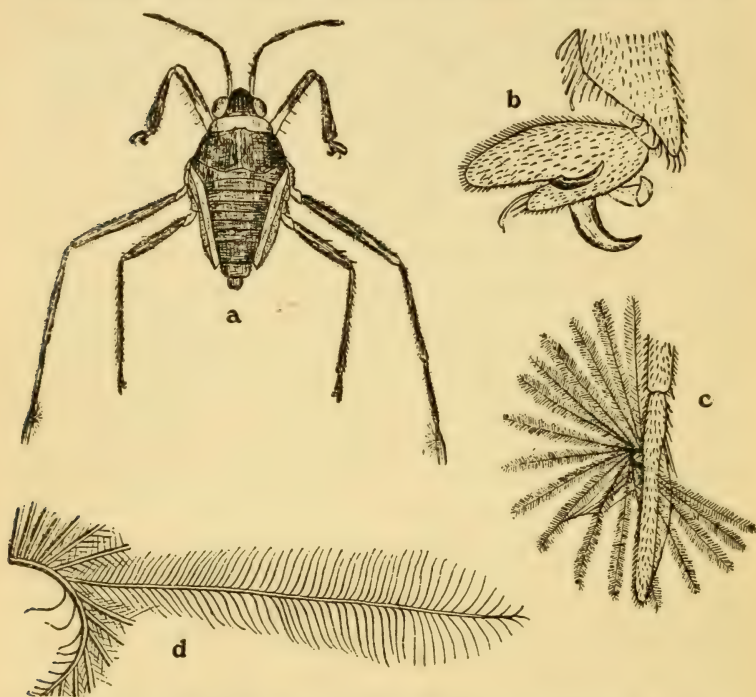


FIG. 74.—*a*, Veliid Marine Bug (*Trochopus plumbeus*), Jamaica,  $\times 10$ . *b*, fore foot with anchoring claws; *c*, intermediate foot with "wheel" of feathered bristles,  $\times 45$ ; *d*, portion of "wheel,"  $\times 150$ . After G. H. Carpenter (*Ent. Mo. Mag.* 1898).

large number of aquatic insects, must be of especial value to those that venture on the surface of the sea.

The true pond-skaters (*Gerris*) with their elongate slender legs are, as we have seen, among the most specialised of freshwater insects that live on the surface-film. Members of a related genus, *Metrocoris*, with several species on the

freshwaters of the eastern tropics, are remarkable for the shortening of the abdomen, beyond which the wings, when at rest, extend for a considerable distance. Examples of *Metrocoris*, found on the surface of estuaries and harbours are often wingless, and these were supposed to belong to a distinct genus (*Halobatodes*) until F. Meinert (1888) showed that at least some of them must be regarded as "undeveloped forms"—that is abnormally wingless adults—of various kinds of *Metrocoris*. Such insects suggest therefore the transition towards an entirely wingless condition, and this state is characteristic of the remarkable genus *Halobates* (Fig. 75), whose members, not only marine but usually oceanic in their habitation, are, as might be expected, very greatly modified in form. Of small size—few species attain a length of  $\frac{1}{4}$  in.—they are smoothly ovate (Fig. 75), dark and convex above, paler and flattened beneath, the whole body covered with a dense velvety pile. The moderately strong fore-legs (Fig. 75, *c*) bear curved claws, set in a cleft of the foot, by which they can anchor to floating objects. Owing to a great backward extension of the middle region of the thorax, the intermediate and hind legs come to be inserted close together (Fig. 75, *b*); they are very long and slender with rigid thighs and shins. The shin and long first foot-segment (*d*) of the intermediate leg are provided with a delicate fringe of long hairs, a beautiful adaptation for water-surface walking. As the abdomen is markedly shortened, the bases of these long legs seem thrust back to the tail end of the body. The extreme modification of body-form in *Halobates* is worked through in every generation, for the young (Fig. 75, *f*) show the normal segmentation of their family and resemble immature *Gerris* rather closely. Most of the known species are described in the "Challenger" monograph of F. B. White (1882). They range widely over the warmer seas of the globe; stray examples have been found in the Atlantic as far north as Spain and Carolina. Their habits have been studied by J. J. Walker (1893) and others. They are most abundant near the shores and have been observed jumping about on seaweed



cast up on the beach of the Red Sea ; but they have been taken by the tow-net in mid-ocean more than a thousand

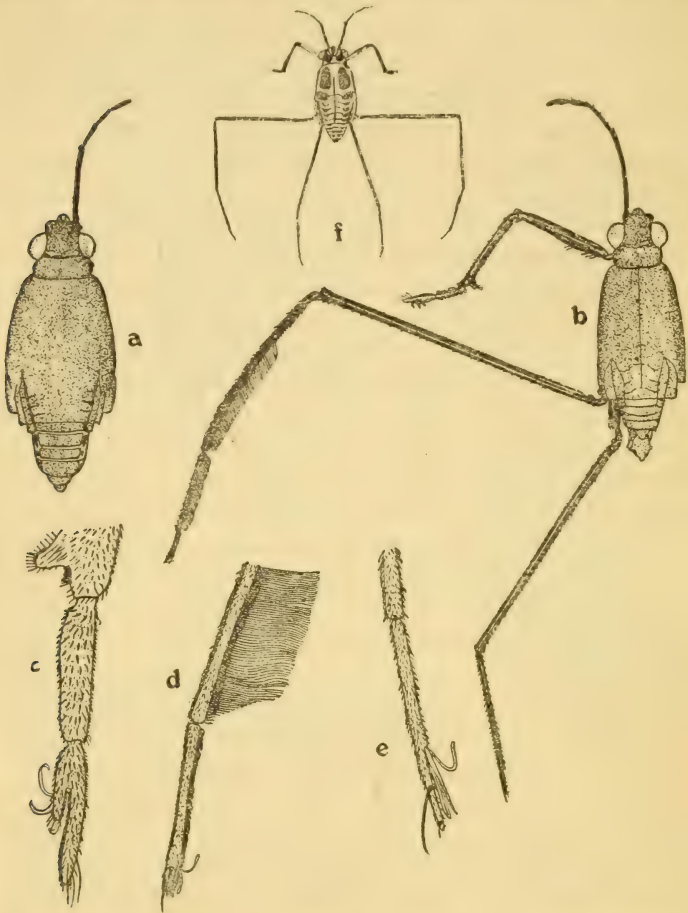


FIG. 75.—*a*, *Halobates herdmani*, Ceylon, female (left feeler and all legs wanting); *b*, male (right feeler and legs wanting),  $\times 5$ ; *c*, fore-foot; *d* and *e*, extremities of intermediate and hind-feet,  $\times 25$ . *f*, Young *H. regalis*, Torres Straits,  $\times 5$ . After G. H. Carpenter, *Rep. Pearl Oyster Fisheries, Manaar* (Roy. Soc.), 1906, V., and *Sci. Proc. R. Dublin Soc.* 1891, vii.

miles from any land. Floating objects serve them as resting-places to which they can anchor, and also as food, when they

cling to a dead jelly-fish and suck its juices. Of their movements Walker writes: "In tropical latitudes when a sailing ship is becalmed or a steamer stopped in a perfectly calm sea, it is not long before little whitish creatures are seen rapidly skimming over the glassy surface with a sinuous motion. . . . A heavy swell, provided the weather is calm, does not prevent their appearance, but with the ripple caused by the slightest breeze they vanish at once. . . . Sometimes they were to be found in plenty on the narrow belt of smooth water to leeward of the ship when not one was to be seen on the windward side." The behaviour of captured specimens in a vessel of sea-water was watched. "On the approach of the finger or a pencil they dive readily and swim with great facility beneath the surface, the air entangled in the pubescence giving them a beautiful appearance like that of a globule of mercury or polished silver. This supply of air must be essential to the existence of the insects which must pass a large part of their life beneath the surface of the sea diving into undisturbed water in rough or even in moderate weather, and coming up again only when it is absolutely calm." But little is known about their breeding habits. Their reddish eggs are large as compared with the size of the mother, who may carry two or three about attached to the underside of her body. The floating feather of a sea-bird picked up in the Pacific Ocean off the Galapagos was found to be covered with masses of *Halobates*' eggs surrounded by a gelatinous envelope. H. C. Delsman (1926) has lately recorded the presence of thousands of the eggs on various objects floating in the Java Sea—seaweeds, *Spirula* and *Sepia* shells, wood and cork, in addition to feathers, yet only twenty-five eggs have been detected at once in the body of a single female. Doubtless many females lay their eggs on one convenient floating nest, for these wonderful little insects are gregarious in their manner of life. Of other marine Hemiptera mention can only be made of the minute but heavily built *Hermatobates*, with hairy body, very stout fore-legs, and abdomen still more reduced than *Halobates*, so that the

haunches of the hind-legs are behind the tail segment. These little bugs crawl on coral reefs, shelter beneath large dead bivalves ten feet below high-water mark, or skim over the surface of the sea in the channels north of Australia and on the coast of East Africa. Their adaptations for marine life are somewhat similar to those of *Halobates*, but they do not appear to venture far out on the waters of the ocean. The modification of these members of the typically aerial class of insects for life in or on the salt water makes them of great interest among the assemblage of "small and great beasts" that dwell in the shallows, the depths and the expanses of the wide sea.

In this survey of the adaptation of insects to the various haunts in which they live some reference has been made to the correspondence of their life-cycle to the changes of the seasons. Some examples that illustrate especially this correspondence may now be given. In tropical regions where insect life is most abundant there may be comparatively slight seasonal change during the course of the year, and generations of a species of insect follow each other without any special need of adaptation to meet marked variations in temperature or humidity. It is rather in the temperate regions of the globe, and in the far north and south, where a proportion of all resident living creatures have to survive a winter of more or less severity, that seasonal adaptations can be most readily and conveniently studied.

Examples taken from among the insects of our own country serve well, therefore, for a discussion of this aspect of insect life. A general survey of the relation between insect life-histories and the course of the seasons demonstrates that the creatures' life-cycles are definitely adapted to the changes of temperature through the year and the resulting changes of conditions of the surroundings, especially with regard to the rise and fall in the abundance of vegetation that affect the food supply. It is evident that insects resident in our northern regions must be able to survive the winter in some stage of their life-history, and among a variety of insects of different groups we find all stages—



egg, early or late larva, pupa, or imago—adopted as the winter form of the species. K. G. Blair, in a suggestive discussion (1921) on the subject, points out that the egg and pupa, both passive, might seem the most suitable stages for the cold season when the food of many insects is scarce or unobtainable ; yet “ these stages are in reality periods of histological activity,” for the embryo may then be formed in the egg-shell and the imago reconstructed beneath the pupal cuticle. It is not therefore surprising “ that many insects have adopted one of the physically more active, though physiologically comparatively quiescent, stages, the larva or the imago, as that in which to pass the winter.” While the life-cycle of many insects is rigidly adapted to seasonal change, as it lasts just twelve months, and the creature reaches the same stage of growth at the same time every year, in many others there are two or more life-cycles in the year, or the rate of development is retarded so that several years are necessary for the appearance of a new generation. Thus it may come to pass that the wintering stage of the life-history is not found only in the winter, or that during the cold season different members of the same species may survive in different stages of growth.

In previous chapters examples have been given of insects of different orders that pass the winter in the adult stage. Such are the large bright-hued vanessid butterflies, like *Aglais urticae* (the “ Small Tortoiseshell ”) or *Vanessa io* (the “ Peacock ”), also queen-wasps and bumble-bees, and a large variety of beetles of different families. Among the last-named, some ground-beetles (Carabidae) and rove-beetles (Staphylinidae) are at least intermittently active, pursuing and devouring smaller insects that may be available as winter prey ; but click-beetles (Elateridae) and many small jumping leaf-beetles (Chrysomelidae) such as the notorious “ turnip-fly,” remain quiescent under stones or clods of earth. Wasps and bumble-bees are passive throughout the winter and afford examples of true hibernation, “ a torpid condition,” as Blair remarks, “ during which no food is taken, no energy expended in movement, and

respiration and all other vital functions are reduced to a minimum." A hibernating queen-wasp reverts to the attitude of a pupa, with her legs bent so that her feet point backwards; her wings are "folded ventrally between the second and third pairs of legs." She rests in some sheltered nook, maybe clinging to a stem or grass-blade with her strongly adducted mandibles. One may find such wintering queens between the stones of a loosely built wall on a high hill-side or in the crack of a window frame in a suburban house. If roughly disturbed in the latter situation she may be sufficiently aroused to use her sting, but the wound inflicted will be comparatively feeble. The vanessid butterflies sometimes find winter-quarters in human habitations; a "Small Tortoiseshell" may mildly disturb a church congregation by fluttering down from the rafters during service-time. But these insects usually frequent hollow trees, the overhanging eaves of sheds, and similar shelters where the chill of open-air conditions will forbid the too early close of their winter sleep. An exceptionally warm and sunny winter's day may, however, lure some hibernating butterflies to leave their shelters probably with disastrous result. Of the British moths hibernating as adults, Blair mentions that the handsome noctuid *Scoliopteryx libatrix* and the grey geometer *Triphosa dubitata* are often found abundantly in winter "on the walls and roofs of the caves, which they shared with numerous gnats and Long-eared Bats."

As might be expected, the egg serves as the wintering stage for many insects, though in some of these the embryo may complete its development in autumn, so that the creature ought rather to be described as an "unhatched larva"; this condition is found, for example, in *Lymantria monacha*. The wingless female of the "Vapourer" (*Orgyia antiqua*), another moth of the same family, emerges in autumn from her cocoon attached to a tree twig, rests on the cocoon during the approach and mating of the active brown-winged male, then lays on the silk her batch of cylindrical eggs, on which before her death she sheds from her body hairs

perhaps serving as a protection. Not until the sprouting of the young leaves in spring-time affords promise of food-supply do the little bristly caterpillars come out of their egg-shells. Hard-shelled winter eggs usually oval in shape are especially characteristic of the plant-sucking aphids or greenfly. These are laid in the autumn on the twigs of the food-plant by the females of the last generation of the year after pairing with males of the same brood. The black shining eggs of the apple aphids are, despite their small size, almost conspicuous on the bare branches through the winter; from them are hatched in spring the "stem mothers" earliest of the virgin generations. Yet the normal restriction of the virgin greenfly to the spring and summer months is not always observed. The well-known Woolly Aphid of the apple (*Schizoneura lanigera*), the original wintering stages of which are eggs on elm trees, often carries on successive virgin generations through the cold season, the insects enduring because they are protected by their dense waxy secretion, and because they often shelter in deep cracks and crevices of the bark of the apple branches, or even penetrate into the core-cavities of such apples as are open at the "eye" end of the fruit.

A large number of insects of different orders winter as larvae, and among these there is great variety as to the particular larval stage—whether early, median, or late—that carries the race over the cold season. Insects with a larval life prolonged over several years must obviously survive several winters at successive periods of their lives, and such generally live and feed in situations which are not subject to great changes of temperature. Thus the long-lived aquatic larvae of mayflies and dragon-flies continue from year to year in the relatively equable temperature of their freshwater home. Among beetles the "wireworm" grubs of click-beetles and the heavy larvae of chafers are feeding on roots in the soil if the weather be mild, but they may burrow deeply in order to escape the effects of severe frosts. Among larvae of Lepidoptera, the large slow-growing caterpillars of the Goat Moth (*Cossus*) pass the winter in their



burrows within the timber of trees. All these live in surroundings where they are to a great extent protected from extreme atmospheric cold.

Some Lepidoptera pass the winter in the first stage after hatching. The white-winged black-spotted Small Ermine Moths (*Hyponomeuta*), that emerge about July from the cocoons among the masses of web on hawthorn bushes, where the caterpillars fed through spring and early summer, lay on the twigs their flattened eggs covering them with a gummy secretion which hardens to form a delicate but firm protective film. Beneath this the caterpillars are hatched from their eggs, and remain sheltered throughout the autumn and winter, coming out in spring to feed on the young foliage and spin their collective web of silk over the branches. The conspicuous cream and yellow, black-spotted Magpie Moth (*Abraxas grossulariata*) is on the wing about the same time of year as *Hyponomeuta*, and the females lay eggs on a great variety of shrubs; the caterpillars are well known devourers of gooseberry and currant leaves in fruit-gardens. The young caterpillars, though hatched at a season when there are still many leaves on the bushes, do not feed, but seek almost at once for winter-shelters such as rolled-up leaves, crannies of bark, or cracks in walls, where they remain until the onset of spring incites them to come out and begin their voracious feeding on the foliage, as a result of which they pass through their successive larval stages and become fully fed in about a couple of months. Another familiar and conspicuous garden insect, the Tiger Moth (*Arctia caia*) hibernates as a half-grown caterpillar. The brilliantly winged adults lay their eggs in July and August; the newly hatched larvae begin immediately to feed and undergo one or two moults before the winter. In spring they begin to feed again and the full-grown "woolly bear" or "hairy outhit" is often seen in May or June crawling on garden paths. The hairy clothing of this and other insects that survive the winter as larvae may probably be regarded as of protective value against cold conditions. The big hairy caterpillar of the Fox Moth

(*Lasiocampa rubi*) becomes fully grown before it hibernates, and does not feed after awakening to fresh activity in the spring, though it drinks water and suns itself before spinning its cocoon and pupating. The destructive caterpillars of the Codling Moth (*Carpocapsa pomonella*) after feeding within young apples, seek shelter under loose pieces of bark and spin their cocoons there, often as early as midsummer ; yet they remain unchanged through the winter and do not pupate until the succeeding spring. A prolonged rest and hibernation in the final larval stage is characteristic also of many sawfly caterpillars, which spin their cocoons in autumn, at or below the surface of the ground and wait for the return of spring to assume the pupal stage. Among the Burnet Moths (*Zygaena*) H. Burgeff (1910) has shown that the caterpillar hibernating in its fourth stage assumes a specially modified form ; after the last moult of the year it appears with an abnormally small head and dull-coloured body, and then passes into the winter sleep, after which it drinks, swells to a larger size, and moults again, appearing in its final stage with the usual bright yellow and black livery of its group. The winter habits of such Owl Moths (*Noctuidae*) as the Turnip Moth (*Agrotis segetum*) and its allies, are especially interesting on account of the plasticity in adaptation that they exhibit. The dull, brown-winged adults are flying in the June evenings and their greyish caterpillars feed on various herbs of the field, usually burrowing in daytime and eating shoots at the ground level by night. Thus the habit of burrowing for shelter and food is normal to these larvae, and they carry it on through the winter, except that during hard frosts they go deep into the soil. Most of the *segetum* caterpillars in our countries remain thus intermittently active through the winter and pupate in spring in an earthen chamber in the soil. But a minority of them grow faster than the rest, so that they are ready for pupation in early autumn, and the moths of a partial second brood emerge in September. The offspring of these join the older wintering larvae in the soil and grow fast enough to complete their transformation about the

same time as those which started several months ahead of them.

The caterpillars of other noctuids—the Cabbage Moth (*Mamestra brassicae*) for example—are fully grown in autumn, and by October or November are lying as pupae buried in their earthen chambers until the time for emergence next season. The pupal is the characteristic wintering stage of many insects, our common White Butterflies (*Pieris*), for example, whose angular pupae, supported by the pad of silk to which the hooked tail-region (cremaster) of the pupa is anchored, and by a silken girdle around the waist, may be seen on tree-trunks, palings, and such resting-places from October to November until April or May, when the spring butterflies emerge. While the Turnip Moth and its allies are partially double-brooded, only a minority of the race completing their transformations in less than a year, the White Butterflies are regularly double-brooded, the caterpillars hatched in spring pupating during the summer so as to develop into a hot-season brood of butterflies in July and August. Enough examples have now been given to illustrate in how many respects the life-cycles of insects are fitted to the circle of the seasons, not the structure only, but the habits of the creatures in the various stages of their growth being adapted so as to ensure the survival of enough individuals to provide for the continuance of the race, while the endlessly diverse ways in which the adaptation is brought about suggests the power of adjustment to new conditions. To this power there are, however, definite limits. Early in this chapter reference was made to the yearly immigration into our islands of the Painted Lady Butterfly (*Pyrameis cardui*). C. B. Williams (1923-4) describes vividly the northward and westward flight of these insects from Egypt over the Mediterranean, giving reason for believing that the starting-place of their immigration is much farther south and that they occasionally travel northward as far as Iceland. Abundant almost every summer in our countryside, these beautiful insects leave no progeny because their winged adults succumb to the conditions even of our milder winters.



Similarly another familiar member of the Lepidoptera, the Death's Head Moth (*Acherontia atropos*) invades the country every summer in numbers ; its caterpillars are hatched, grow, and pupate in the soil, but the combined coolness and damp of our winters apparently kill them all. The migrant powers of such insects give promise of wide extension of their permanent range, but such promise is unfulfilled if they cannot adapt themselves throughout the year to the climatic conditions of the occupied territory.

## CHAPTER XI

### CLASSIFICATION

THROUGH the preceding chapters of this account of the Biology of Insects reference has necessarily been made to the orders, families, genera, species into which Insects are divided. The study of animals from any point of view involves the use of some classification, and it may be convenient at this stage of our discussion to consider more systematically than hitherto the various groups of insects. The object of systematic zoology is to express those degrees of likeness and difference which become apparent as the creatures are compared with each other. Here we are concerned with such comparisons so far as they afford help in understanding the different insects' ways of life, as well as the elucidation of relationship between groups which is the goal of systematic study.

At the end of Chapter I. (pp. 13-14) a concise definition of the Insects as a class was given. We noticed that insects form a distinct class of that great primary division or Phylum of animals called the Arthropoda. Insects resemble Crustacea (lobsters, shrimps, crabs, barnacles), Arachnida (spiders, scorpions), Chilopoda (centipedes), and Diplopoda (millipedes), in their segmented, cuticle-clad body and jointed limbs. They differ from these other classes in the restriction of the well-developed locomotor limbs to three pairs, and usually in the possession of wings, for the great majority of insects acquire the power of flight when adult. Some, however, never attain to this fullness of development. It might therefore be suggested to start classifying insects by setting those which have wings over against those which

never develop any. But in several lines of study we have come across the interesting fact that some individuals of the same kind may be winged and others wingless, even the young of one mother, hatched from eggs laid, or born at the same time may grow into either winged or wingless adults, like the aphids or the ants, or like the scale-insects and those moths in which the males have wings and the females none. As such wingless insects all belong to groups typically winged, there can be no hesitation in regarding the wingless condition as "secondary." The wingless aphid is obviously closely akin to her winged sisters, she has, as it is commonly expressed, "lost her wings," and a classification that depends rigidly on the presence or absence of wings is quite clearly unnatural, for it would obscure rather than express the relationship between the various groups. Thus we incidentally reach the highly important conclusion that a classification can be regarded as satisfactory only in so far as it does indicate the mutual relationships of the creatures classified. Again, we noticed in our discussion of growth and development (p. 164) that certain entire groups of insects, as lice and fleas, are wingless, though they are shown by their form to be allied to winged groups. They also, therefore, furnish examples of "secondary" winglessness which may characterise not some members only of a family or an order, but all.

There are, however, certain families of entirely wingless insects which may be distinguished from others by very definite and important additional characters. The bristle-tails and springtails have, in the adult state, paired limbs on several at least of their abdominal segments, and they have mandibles which resemble those of Crustacea much more nearly than those of typical insects (Figs. 52, *b*, 79, *c*, *e*). These associated characters suggest that the wingless condition of such insects is not secondary but primitive, and that it is reasonable to separate these bristle-tails and springtails (as Apterygota) from all the rest of the class (Pterygota) in which the development of wings is a typical character, though wings may be absent in many



individuals of certain species or in a whole group. This is a preliminary division of the insects which seems truly to indicate such differences as express degrees of relationship. It is instructive to recall that in classifications of a century and a half ago bristle-tails and springtails were grouped with Crustacea and Centipedes as "Aptera." No doubt now remains that, although they show certain crustacean affinities they must be definitely included in the same class as the winged insects, but recognised as a distinct sub-class. This systematic treatment of the Apterygota is now generally followed by entomologists.

The bristle-tails and springtails form the vast majority of the Apterygota, and the features which distinguish the one group from the other may serve as samples of the discrimination between two exceedingly well-defined orders of insects. Bristle-tails have long, many-jointed feelers, usually possess compound eyes, and a typical insectan abdomen of ten segments the last of which bears a pair of conspicuous appendages, usually long and many-jointed like the feelers; as many as eight of the other abdominal segments may carry paired limbs—typically unjointed stylets—and usually there are prominent reproductive processes. Springtails, on the other hand, have relatively stout feelers with four (rarely six) segments, their eyes are always of the simple ocellar type, and the number of abdominal segments is reduced to six, of which only the third, first, and fourth bear appendages concerned with locomotion and forming respectively the ventral tube, the catch, and the spring. The bristletails (Fig. 52, *b*) are therefore separated as an order (Thysanura) from the springtails (Collembola, see Figs. 66, 70).

Our review of the development of winged insects after hatching (Chap. VII) showed a striking divergence in the method of wing-growth, between such groups as cockroaches, grasshoppers, dragon-flies, and bugs, in which the wing-rudiments appear early outwardly on the thorax, increasing in size at each moult, and on the other hand, such groups as the beetles, two-winged flies, butterflies and

moths, wasps and bees, in which the immature insect is a larva, differing markedly in aspect from its parent, with the wing-rudiments developing hidden in inpushed pouches, to become visible only at the resting or pupal stage of the life-history. These facts may be expressed in our classification by dividing the winged insects (Pterygota) into two subclasses: (1) the Exopterygota whose members practise the open type, and (2) the Endopterygota whose members show the hidden type of wing-growth. This important systematic distinction is due to D. Sharp (1898). Each of these subclasses comprises a number of orders, the distinction between which depend upon the nature of the jaws, whether for biting or sucking, upon the form, texture, and nervuration of the wings, upon the presence or absence of tail-processes (cerci), and upon details of the life-history such as the typical form of the larva and pupa. For detailed discussion of these subjects systematic treatises on entomology should be consulted. Here it will suffice to give such brief definitions of the orders as may serve for necessary purposes of reference from the other chapters of this book.

Class **INSECTA** (or Hexapoda) (see definition, Chap. I,  
pp. 13-14)

### Sub-class I. **APTERYGOTA**

These are wingless insects in which the wingless condition seems to be primitive. When the jaws are typically developed the mandibles are of the crustacean type, and there are paired superlinguae or paragnaths in front of the tongue. The abdomen carries a varying number of paired limbs.

#### Order 1. **THYSANURA**

These are wingless insects known as Bristle-tails, with elongate, many-jointed feelers, usually compound eyes, and abdomen of ten segments, many of which usually carry

paired limbs, the hindmost often elongate and many-jointed cercopods (Fig. 52, *b*).

### Order 2. PROTURA

These are very minute insects without feelers, wings, or cercopods. The jaws are modified for piercing and sucking, and the three hinder segments of the abdomen are not developed until after hatching.

### Order 3. COLLEMBOLA

The Springtails have feelers with only four (rarely six) segments; there are no compound eyes. The abdomen has only six segments, the first of which carries a ventral tube, the third a catch, and the fourth a spring—all these three structures being modified from paired appendages (Figs. 66, 70).

### Sub-class II. EXOPTERYGOTA

These are winged (or secondarily wingless) insects in which the wing-rudiments appear outwardly at an early stage on the second and third thoracic segments and increase in size after each moult. They are generally active throughout growth, but in some groups the wing-rudiments develop beneath the unshed cuticle of a previous instar and there may be a resting stage before the final moult.

### Order 4. DERMAPTERA

The Earwigs and their allies have the wings (when present) modified so that the forewings become shortened horny pads beneath which the delicate membranous hindwings can be folded when not in use. The mandibles are of the normal biting type, and there are fairly prominent superlinguae (Fig. 6). The tail-appendages are usually modified into a forceps, but in one family are jointed cercopods. The genital ducts have no chitinous lining.



## Order 5. ORTHOPTERA

The Cockroaches, Leaf-insects, Stick-insects (Plate I, A), Grasshoppers, Locusts, Crickets, and other insects comprised in this order have biting mandibles, forewings firm in texture and relatively narrow, the ampler hindwings being folded beneath them when at rest. There are jointed cercopods at the tail-end and (in the female) an ovipositor (Fig. 36, A).

## Order 6. PLECOPTERA

The Stoneflies have biting mandibles, though these are often reduced, and two pairs of membranous net-veined wings, the hind pair usually folding ; there are tail cercopods often elongate. The insects develop from aquatic nymphs (Plate X, B) which live submerged in streams and breathe through tufted gills on the thorax.

## Order 7. ISOPTERA

The Termites (Fig. 64) and Embiids have the two pairs of wings closely alike and incapable of folding (many forms are quite wingless). They have biting jaws and short cercopods.

## Order 8. CORRODENTIA

The Booklice and their allies have their wings (when present) delicate and membranous, the forewings both longer and broader than the hindwings. There are biting mandibles, and the inner lobes of the maxillæ are elongate "picks." Cercopods are absent.

## Order 9. THYSANOPTERA

These insects, generally known as Thrips, have short feelers, and the jaws adapted for piercing and sucking, the mandibles being slender and needle-like. The wings of both pairs are delicately membranous, narrow, and fringed.

Cercopods are absent. Immature Thrips resemble generally their parents, but there is a passive stage before the final moult.

### Order 10. MALLOPHAGA

The Biting Lice are wingless, parasitic insects with short feelers, reduced eyes, biting mandibles, and maxillary palps. There are no cercopods. They live on birds and mammals.

### Order 11. ANOPLURA

The Sucking Lice are wingless parasites with short feelers and a highly modified tubular, suctorial mouth. They live on mammals and the feet, each with a single strong claw, are formed for clinging to the hosts' hair. Cercopods are absent.

### Order 12. HEMIPTERA

These are insects with jaws formed for piercing and sucking, the needle-like mandibles and maxillae working to and fro in a dorsal groove extending along the elongate beak-like labium (Fig. 8). There are no cercopods, but the female has often a well-developed ovipositor.

#### Sub-order i. HETEROPTERA

The Bugs have the beak arising towards the front of the head, and the forewings (except for a membranous apex) firm in texture. The young insects closely resemble their parents (Fig. 4).

#### Sub-order ii. HOMOPTERA

The Cicads (Fig. 44), Froghoppers, Aphids (Fig. 42), Suckers (Fig. 43), Scales, and allies have the beak arising far back towards the forelegs. The forewings and hindwings are usually alike in texture. The young often differ from their parents, and pass through a

marked transformation with a resting stage before the final moult.

### Order 13. EPHEMEROPTERA

The Mayflies are delicate insects with short feelers, vestigial jaws, and net-veined wings, the forewings markedly longer and larger than the hindwings. There are long jointed cercopods and the genital ducts have no chitinous lining. The young are aquatic nymphs with the essential features of the Thysanura, the abdominal limbs modified into tracheal gills (Fig. 52, A). There is an aerial subimaginal stage before the final moult.

### Order 14. ODONATA

The Dragon-flies are strong insects with short feelers, large eyes, and powerful biting jaws. They have four net-veined wings of glassy texture and an elongate abdomen with rigid, unjointed tail processes, ovipositor in the female, and genital armature on the second segment in the male. The immature insects are aquatic larvae with varying adaptations for breathing dissolved air.

#### Sub-order i. ANISOPTERA

This group includes the large, robust dragon-flies in which the hindwing is markedly broader than the forewing at the base. The larvae breathe by means of tracheal gills on the walls of the hind-gut, and their three tail-processes are rigid.

#### Sub-order ii. ZYGOPTERA

This group includes the slender damsel-flies whose forewings and hindwings are alike narrow at the base. The larvae breathe by means of their three elongate tail-processes which are flexible and often flattened.



## Sub-class III. ENDOPTERYGOTA

These are winged (or secondarily wingless) insects, developing from larvae that are usually much unlike the adults, with wing-rudiments growing in hidden pouches pushed inwards from the body-wall (Fig. 46), so that they become apparent only in the penultimate stage, which is a true pupa, usually quiescent and taking no food. Many other organs of the adult arise before and during the pupal stage from groups of cells (imaginal discs) present in the larva, so that there may be much reconstruction in the course of development.

## Order 15. COLEOPTERA

The Beetles have strong biting mandibles, a freely movable prothorax, and the hard, firm forewings modified into sheaths (elytra) beneath which the membranous hindwings can be folded when not in use. (In many beetles the hindwings are vestigial or absent.) Beetle larvae vary greatly in form from the active, firm-coated, long-legged campodeiform type to the soft-coated eruciform grub with legs reduced or wanting (Figs. 47, 48, 49). In the growth of some beetles the former type is succeeded by the latter (hypermetamorphosis). The wings and limbs of a beetle pupa (Fig. 47, *b*) are free from the body.

## Order 16. NEUROPTERA

These insects have biting jaws and two pairs of membranous net-veined wings usually alike in form. There are no abdominal cercopods. The larvae are usually campodeiform and the pupae free in type.

## Sub-order i. MEGALOPTERA

The Alder-flies and Snake-flies have the wing-neuration comparatively simple, and their larvae have biting mandibles like those of the adults.

## Sub-order ii. PLANIPENNIA

The Lacewing, Golden-eye, Antlion flies and their allies have wings with more complex neurulation, and the larvae have their jaws slender, curved, and grooved, specially adapted for sucking the juices of weaker insects on which they prey.

## Order 17. MECOPTERA

The Scorpion-flies and allied families have the head prolonged in front into a beak at the tip of which is the mouth with its biting jaws. The wings are long and narrow, both pairs closely alike in form and neurulation; there are short abdominal cercopods and (in the females) a long ovipositor. The larvae (Fig. 78) are of the caterpillar type with eight pairs of abdominal pro-legs in addition to the six normal thoracic legs.

## Order 18. TRICHOPTERA

The Caddis-flies have no mandibles; they suck liquids with their maxillae and labium. They have membranous hairy wings with typical longitudinal neurulation and few cross-nervules; the hindwings are shorter and broader than the forewings, with an anal area. There are no cercopods. The larvae ("caddis-worms") have strong mandibles and long legs; they live under water, sheltering in protective cases of plant-fragments, or stones spun together by silk, and breathe by threadlike abdominal gills. The pupae have strong mandibles and rise to the surface before emergence of the flies.

## Order 19. LEPIDOPTERA

Moths and Butterflies have, as a rule, no mandibles, and the maxillae are specialised, elongated, and grooved to form a flexible sucking trunk (Fig. 9). The body and wings are covered with flattened scales, and the neurulation is mainly longitudinal. The forewing is markedly longer than the

hindwing. There are no cercopods. The larvae are typical caterpillars with strong mandibulate head, soft-coated body often tubercled and hairy or spiny, with (usually) five pairs of abdominal pro-legs besides the six thoracic legs (Figs. 5, 45). The pupa is rarely free and mandibulate; usually it becomes obtect, with wings and limbs adherent to the body.

#### Sub-order i. HOMONEURA

This group comprises only four or five families in which the hindwing has as many nervures as the forewing. In two of these families the pupa is free and mandibulate.

#### Sub-order ii. HETERONEURA

This group comprises all the rest of the Lepidoptera—perhaps fifty families—in which the radial nervure is simple in the hindwing while in the forewing its normal five branches are present. The pupa is never mandibulate and always more or less obtect.

### Order 20. DIPTERA

The Two-winged Flies have a specialised sucking labium without palps; mandibles and maxillae may serve as piercers (Fig. 7). The forewings only are developed for flight, the hindwings being knobbed halteres ("balancers"). The larvae are eruciform grubs without true limbs, but often bearing pro-legs (Fig. 72, *c*), or headless maggots (Fig. 51).

#### Sub-order i. NEMATOCERA

These are Diptera whose feelers are elongate, with seven or more segments. All the larvae have a definite head-capsule and the pupal cuticle splits longitudinally for the emergence of the fly (Orthorrhapha).

#### Sub-order ii. BRACHYCERA

These are Diptera, the terminal region of whose feelers is suppressed so that there appear to be only



three to five segments. In a minority of the families there is a headed larva and the orthorrhaphous type of pupa. Most Brachycera have headless maggots as their larvae; the final larval cuticle is not shed but hardens and contracts to form a protective case (puparium) for the pupa. The puparium (Fig. 54) splits open by the breaking away of an anterior rounded lid to allow for the emergence of the fly (Cyclorrhapha).

#### Order 21. APHANIPTERA

The Fleas are laterally compressed, parasitic, wingless insects with elongate piercing and sucking jaws adapted for drawing blood from their vertebrate hosts. They have mandibulate and legless eruciform larvae (Fig. 67, *b*).

#### Order 22. STREPSIPTERA

These are very small insects parasitic on other insects (mostly Hemiptera and Hymenoptera). The males are active and winged, the hindwings being membranous, and the forewings reduced to balancers. The females are wingless and passive, remaining in the bodies of their host-insects. They develop with a hypermetamorphosis, a minute active campodeiform larva transforming into a legless parasitic grub.

#### Order 23. HYMENOPTERA

The members of this large order have biting mandibles and the labium adapted for sucking liquids. The forewings are markedly larger than the hindwings, and the nervuration is specialised so as to form a series of small areolets on the wing area. The first abdominal segment is joined to the thorax. Cercopods are present and the female has a strong ovipositor. The larva is eruciform and the pupa free.

## Sub-order i. SYMPHYTA

The Sawflies have no constriction at the base of the abdomen. Their larvae are caterpillars with seven or eight pairs of unarmed abdominal pro-legs (Fig. 76).

## Sub-order ii. APOCRITA

The Gallflies, Ichneumon-flies, Wasps (Fig. 60), Bees, and Ants (Fig. 61) have a strong constriction ("waist") behind the first abdominal segment. Their larvae (Figs. 50, 62) are legless grubs.

In the above summaries of the orders of insects reference has been made to families that are comprised in certain of the orders. A family in a zoological classificatory system is thus a group subsidiary to the order. It is convenient to divide some of the orders (Hemiptera and Hymenoptera, for example) into sub-orders, and many students group together a number of related families into an assemblage called a tribe or a superfamily, intermediate between the order or sub-order and the family. An enumeration of all the families of insects is impossible in this book, but it may be well to follow up our summary of the insect orders and their distinctive characters by giving a few illustrations of the kind of characters on which families are based. These illustrations may be conveniently taken from the Hymenoptera, the latest order in the summary.

There are two well-marked sub-orders of Hymenoptera distinguished by structural features both in the adult and larval stages. Of these the Symphyta are a relatively small group including only four or five families, while the Apocrita are a very large and dominant group including twenty families or more.

Among the Symphyta the two most important families may suffice. The Tenthredinidae (Sawflies) comprise several thousand species of insects which, in addition to the sub-ordinal character of the broad-based abdomen,

agree in having a prothorax much reduced in size and two spines on the shin of each fore-leg; the female's ovipositor is very well developed, but never projects far beyond the tail-end of the body. The larvae are of the caterpillar type with seven or eight pairs of pro-legs besides the six thoracic legs; most of them feed openly on the leaves of plants (Fig. 76).

The Siricidae (Giant Sawflies, Horn-tails, or Wood-wasps) have the prothorax less reduced, the shin of each

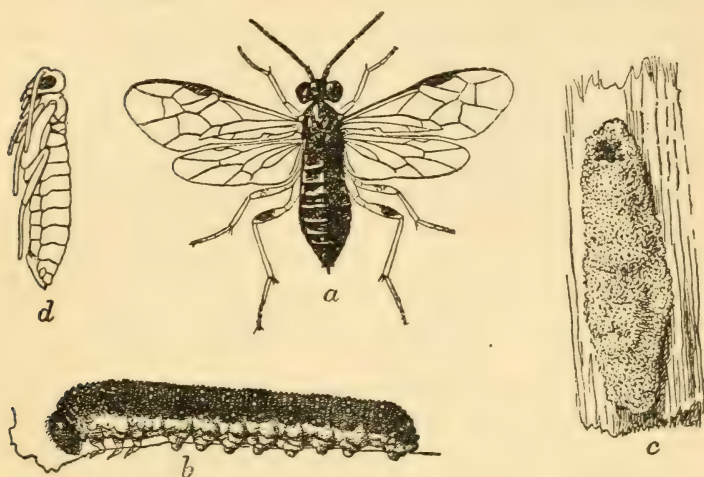


FIG. 76.—*a*, Sawfly (*Emphytus canadensis*), female, North America; *b*, caterpillar (side view); *c*, cocoon; *d*, pupa (side view),  $\times 4$ . From F. H. Chittenden (*U.S. Dept. Agric. Ent. Bull.* 27, 1901).

fore-leg with only one spine, and the hind abdominal segment produced backwards into a spine-like process. This in the female is very long, and the prominent ovipositor extends below it. By means of this ovipositor borings are made in wood and the eggs deposited there. The larvae have very short thoracic legs and no pro-legs. There are less than a hundred species of this family known—a great contrast as compared with the multitude of Tenthredinidae.

The Apocrita form that sub-order of Hymenoptera whose members have a marked constriction or waist behind



the foremost abdominal segment, which apparently belongs to the thorax. It is worthy of note that this structural character facilitates the free and accurate movement of the abdomen, so that the backwardly directed ovipositor can be brought to bear on any spot where the female can profitably practise egg-laying. It has been mentioned that there are many families of Apocrita and for distinguishing these various structural features are of service to the student. The pronotum or dorsal shield of the prothorax extends backwards at the sides as far as the tegulae at the bases of the forewings in most Symphyta, and this is also seen (Fig. 77, *a*) in several large families of the Apocrita—for example, in the Cynipidae (Gallflies), the Proctotrypidae (a large family of small flies with parasitic larvae), the Pompilidae (a family of digging-wasps that usually provision their nests with spiders), the Vespidae or true wasps (Fig. 77, *a*), and the Formicidae or Ants. On the other hand, the pronotum is relatively short (Fig. 77, *b*) in the Chalcididae (flies with parasitic larvae), the Sphegidae (digging-wasps that provision their nests with caterpillars and other insects), and in the Apidae (bees). The trochanter or small second segment of the leg is divided into two regions (Fig. 77, *d*) by an apparent joint in the Ichneumonidae, Chalcididae, and Proctotrypidae, but is simple in the Pompilidae, Sphegidae, Vespidae, Formicidae, and Apidae. Most of these Hymenoptera with undivided trochanters (Fig. 77, *c*) have the ovipositor of the female modified into a sting, and are therefore collectively known as Aculeata. The true Wasps (Vespidae) are known from the Pompilidae by the longitudinal folding of the forewings when at rest. Ants are readily recognised by the second (apparently first) abdominal segment, the “waist,” forming a prominent “node,” and in many groups of ants the third abdominal segment is similarly modified. The Apidae or bees are distinguished by their broad basal foot-segments and their plumose hairs; characters which are of great importance in connection with their habit of gathering the pollen of flowers for food. From these examples it can be seen that a family of insects

is distinguished by a combination of characters which all its members have in common. It is necessary, however, to realise that classifiers of insects often differ among themselves as to what they mean by a family. Several of the groups just mentioned as families are regarded by many writers as "superfamilies"; J. H. Comstock, for example, in his recent handbook (1924) reckons eight families of Symphyta and forty of Apocrita in a systematic treatment of the Hymenoptera.

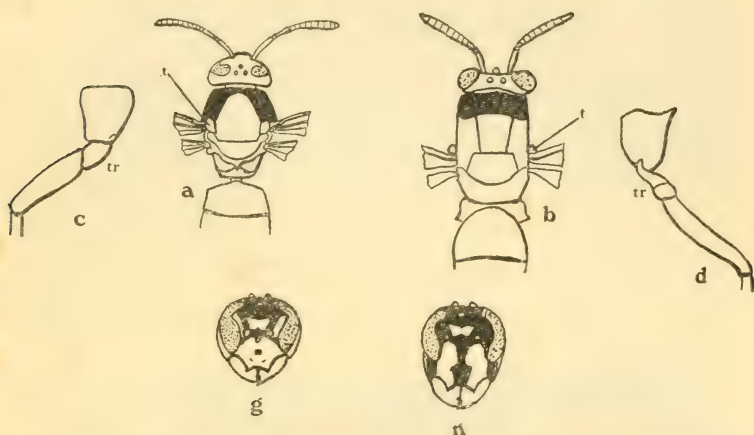


FIG. 77.—*a*, Dorsal aspect of front half of Wasp (*Vespa*), showing prothorax (black area) reaching back to tegulae at wing-bases; *b*, corresponding region of a Chalcid, in which the prothorax (black area) does not extend backwards; *c*, part of leg of *Vespa* with undivided trochanter (*tr*); *d*, the same of a Chalcid with divided trochanter; *g*, "short" face of a ground-wasp (*Vespa germanica*); *n*, "long" face of a tree-wasp (*V. norvegica*). Magnified.

Every family of insects comprises a number of genera; rarely do we find a monotypic family with only one genus. It may be noted that a family name in systematic zoology is formed from the root of the generic name with the termination *-idae*. Thus the family name for the true Wasps—Vespidae—is formed from *Vespa*, the name of the typical genus.

In these countries there are two genera of Vespidae, each with several species and each representative of a distinct

sub-family. The genus *Odynerus* includes solitary wasps in which there is no worker caste ; the females usually build nests of earth or of hardened clay (Plate XI, B) wherein they lay their eggs and deposit caterpillars to serve as food for the grubs when hatched. *Odynerus* and other genera of the sub-family Eumeninae have elongate grooved mandibles and a still longer labium ; the shin of each middle leg has a single apical spine and the foot claws are toothed or bifid. *Vespa*, the typical genus of the Vespinae, has relatively short mandibles and a still shorter labium ; the shin of each middle leg has two spines at the tip, and the foot-claws are simple. Most of the Vespinae form true social communities with a worker caste (as described in Chap. IX, pp. 223-4, 234-6), and build nests of a paper worked up from wood (Plates VII, VIII). The differences in the jaws and legs mentioned as distinguishing *Odynerus* and *Eumenes* on the one hand from *Vespa* on the other are typical of the characters that are found to hold through large series of related species, and are therefore of special value in serving to define the genera in which the species are grouped.

From the genus we may now pass to the species, and the British Social wasps (*Vespa*) may serve as examples of specific distinction. The largest of them is the Hornet (*Vespa crabro*) to be recognised not only by its size, but by the predominantly brown hue of its body. Our other species of *Vespa* all have the thorax black and yellow. Two of the six—*Vespa sylvestris* and *V. norvegica*—are “ long-cheeked ” wasps, with cheeks prolonged (Fig. 77, *n*) below the eyes towards the bases of the mandibles, and with shins markedly hairy. Both species build their nests in trees. *Vespa sylvestris* has the face clear yellow with only a small central black spot, while in *V. norvegica* there is a broad central black streak. The other four—*Vespa vulgaris*, *V. germanica*, *V. rufa*, and *V. austriaca*, all of which nest in the ground, are “ short-cheeked,” the base of the mandible close beneath the eye (Fig. 77, *g*), and the shins clothed with short hairs. *V. vulgaris* has usually a broad black band down the



PLATE XI



LARVAE OF BRACONID (*Apanteles glomeratus*) emerging from Caterpillar of *Pieris*.  $\times 4$ .

[J. G. Parker, photo.



NEST OF *Odynerus pictus*.

To face p. 322.]

[H. Britten, photo.



middle of the yellow face, while in *V. germanica* the band is narrow, sometimes reduced to a spot, and there is a black spot on either side below. In both these species and also in *V. austriaca* the yellow and black markings of the abdomen are sharply defined, but in *V. rufa* the edges of the black markings pass into reddish-brown. The face of *V. rufa* is like that of *V. vulgaris*, the face of *V. austriaca* like that of *V. germanica*. These differences of form and pattern between the various kinds of British wasps are of the type used in discrimination of species, and within the same species the characters are fairly constant. There are, however, very definite structural specific characters which become apparent from study of the male genital armature, and these on account of their obvious biological and genetic importance are often of greater value in specific distinction than conspicuous features of colour and pattern. As already mentioned in Chapter IX (pp. 234-5), *V. rufa* and *V. austriaca* are, in the form of the male armature, more closely related to each other than either is to any other British wasp. The males and queens of *V. austriaca*, which appears to have no worker caste, are reared in nests of *V. rufa*, as if the former were a "guest" of the latter, but there is considerable evidence for the view that the two are alternative varietal forms of one species. The British wasps afford, therefore, an illustration of the difficulty often found in deciding whether two distinguishable insects should be regarded as distinct species or as varieties of one species. Where it can be proved that two or more forms may arise from eggs laid by the same parent, or can be traced back through an observed and recorded series of generations to a common ancestry, specific identity becomes certain. But the classifier of insects is often in doubt as to the limits of the groups that he seeks to define as "species," "sub-species," "variety," and "aberration," as well as of the more comprehensive groups known as the genus, the family, and the order. This frequent uncertainty as to definition is one of the fascinating puzzles that confront the student of biology ; while it gives ground to the critic for the charge



that biology is not an "exact" science, it is a limitation that must be accepted when the subject under consideration is life as shown in some of its almost infinitely varied manifestations. Our classificatory scheme, because of its uncertainty and difficulty, becomes a natural introduction to the problems of interpretation which are to be discussed in the following chapter.

## CHAPTER XII

### EVOLUTION

THE scheme of Classification briefly set forth in the preceding chapter is an attempt to demonstrate the varying degrees of likeness and divergence among insects, and it has been repeatedly suggested in this book that these varying degrees of likeness and divergence indicate varying degrees of relationship. Long ago the systematic students of plants and animals sought their ideal classification in a scheme that might be regarded as "natural." For the past sixty years it has been generally realised among biologists that "relationship" between living creatures must not be considered merely a figure of speech, but that the degrees of likeness and difference expressed in a scheme of classification indicate actual natural relationship. The general conception of organic evolution became an accepted principle among naturalists, as is well known, through the work of Charles Darwin (1859), and a sentence from his famous book may be quoted that sums up the meaning of systematic study and its interpretation: "I believe that community of descent is the bond which is partially revealed to us by our classifications." In view of the immense number of different species, genera, and families of insects, differing in the most varied degrees among themselves, the student of insect life finds a reasonable interpretation of the facts of structure and classification in the principle of evolution. The differences of habit and manner of life among insects of the same group, as exemplified in their family and social relations (see Chaps. VIII, IX), suggest that the creatures may be plastic in their behaviour as well as modified in

their form from early ancestral conditions. Like all living creatures whose origin as individuals can be studied, they arise from germ-cells borne in the bodies of parents like themselves. If therefore we reject the evolutionary view of living nature that all insect races have, like individuals, an ancestry, we must needs abandon the attempt to explain the method of their origin. And when we find that the insects of past ages, known to us from remains preserved as fossils in rocks of various periods, differ on the whole from insects of to-day the more markedly the farther the history of the Class is traced back in geological time, we are confirmed in the belief that in "descent with modification"—an age-long series of countless generations through which changes in form, in methods of growth, in ways of behaviour, have been worked out—we have a clue to the problems presented by the life of insects as by the whole realm of organised creatures.

It is easy, then, to accept the general principle of evolution as we seek to understand in a wide view the Biology of Insects, but to work out the principle in detail to fit the immense extent of varied facts and relations becomes increasingly difficult. Insects are of high importance in discussion on these subjects because so many factors, real or supposed, in the general evolutionary progress of living beings have been elucidated through the study of insect life. Considerations of space preclude the survey in this chapter of a great mass of detail, however interesting such may be. We must, however, attempt to discuss in outline, with detail sufficient for elucidation, the two great evolutionary problems about which much difference of opinion has prevailed and still prevails among students. These problems may be defined as (1) The Course of Evolution; and (2) The Factors or Methods of Evolution, among Insects. These problems are not absolutely separable, since various facts and inferences which throw light on the one may be of service in elucidating the other; it will be convenient, however, to consider them in turn, indicating in some degree how they are correlated.



In seeking to trace the course of the development of insects as a class we have to compare the characters of the orders and families as regards structure and life-history so as to determine which groups are the more primitive and which the more specialised. Among all classes of animals there are certain groups which seem clearly to have changed less in the course of time than others. It would obviously be rash and probably quite wrong to infer from this that the more specialised groups are direct descendants of the less specialised. The fact that both grades are living together in the world to-day suggests that they are collateral descendants of forms now extinct. But we are justified in concluding that the more primitive of surviving insects resemble more closely an ancestral stock, more or less remote, than do members of the more specialised orders. The survey of insect classification in the previous chapter indicates the wingless Apterygota as the most primitive of the sub-classes. As insects are the only members of the Arthropoda endowed with the power of flight by means of wings, it is certain that the common ancestral stock of insects and other classes of arthropods were wingless creatures, and that the early insects before they acquired wings had assumed the characteristic insectan distinction between the thorax with its three pairs of legs and the abdomen with its limbs mostly reduced or wanting; the dominance of the thorax as the locomotor centre of the insect seems a necessary preliminary to the development of wings in that region of the body. We feel confident, therefore, in regarding such a bristle-tail as *Machilis* as resembling the primitive stock of the Insecta more closely than any other living type, but we are not warranted in referring to the unknown members of that stock any detailed characters of *Machilis* except those that are clearly indicated as primitive. The body segmentation with its three thoracic and eleven abdominal segments, the crustacean type of mandible, the superlinguae, the abdominal appendages, reduced except the long tail-cerci, all these are thysanuran features which may confidently be claimed as primitive

(Figs. 52, 79). Comparison of Thysanura with the Collembola, the other important order of the Apterygota, indicates that the latter have departed far from the primitive type mainly through a degenerative specialisation, for the number of abdominal segments is reduced to six, three of which normally carry paired appendages, partly fused basally and greatly modified to form respectively the ventral tube, catch, and spring (Fig. 66). That the Collembola are, despite their extreme modification, truly akin to the Thysanura is evident from the fact that one of their most remarkable features—the retraction of the jaws into the head-capsule, a condition associated with a striking specialisation of the maxillae and tongue—is found also in two families of the Thysanura, the Campodeidae and Iapygidae, which are often relegated to a special sub-order and sometimes even to a distinct order, as in the scheme of C. Börner (1904).

When the naturalist tries thus to deduce relationships between groups of animals by a comparative study of their structure, he desires to check his conclusions by knowledge of the past history of the groups as revealed by fossils. As far as the Apterygota are concerned this is impossible because such frail terrestrial creatures as bristle-tails and springtails have little chance of preservation in sedimentary rocks accumulated under water, and our only certain knowledge about extinct Apterygota is derived from some Collembola closely like living types, embalmed in the Baltic amber of early Tertiary (Oligocene) Age. Fragmental remains in rocks of Devonian Age have been referred to the Thysanura, but no reliance can be placed on them as evidence that bristle-tails lived in that remote period. No doubt, however, can be felt that thysanuroid insects were living then, because the existence of winged insects of various types in the succeeding Carboniferous period is abundantly attested by fossil remains.

In our discussion on the growth and transformation of insects in Chap. VII (pp. 160–194) reasons were given for the belief, now generally accepted by all students of the

subject, that the open type of wing-development preceded the hidden type in the evolution of the class ; the Exopterygota as a group are more primitive than the Endopterygota. In all those orders whose members show a marked contrast between the adult and the larva, we recognised evidence for an increasing divergence between the early and the final stage of the life-history (see pp. 183-6). To estimate approximately the relationship between the various orders of winged insects it is necessary therefore to take into account the form of the creature both in the immature and adult conditions.

The orders of winged insects—whether exopterygote or endopterygote—are distinguished mainly, as regards the adults, by the characters of their jaws and their wings, and these are alike structures of great biological importance, as on them respectively depend the feeding and the movement of the creatures. Comparison of the various types of jaws among insects assures us that the mandibulate condition, in which the mandibles are adapted for biting solid food-stuffs, is more primitive than the various modifications of the mouth-parts for piercing and sucking, because biting mandibles of essentially the same form are found in many orders of both the sub-classes of winged insects, in the Orthoptera, Isoptera, Corrodentia, Odonata, Coleoptera, Neuroptera, Mecoptera, and Hymenoptera, for example. The members of these orders agree not only in the build and mode of working of the mandibles but also in the general structure of the maxillae. The parts of a typical maxilla, such as that of an earwig (see p. 18) or cockroach can be recognised in all mandibulate insects whether their mode of wing growth be open or hidden. It is evident, therefore, that such mandibles and maxillae were characteristic of most primitive winged insects and that they have been inherited with relatively minor modifications by a large proportion of the existing orders. The characteristic parts of the hinder pair of maxillae that form the labium can also be recognised in the members of these and other orders ; only in the more highly specialised groups—Coleoptera,



Neuroptera, and Hymenoptera, for example—the basal regions of these latter appendages tend to become more closely united together while the lobes become reduced so that the labium is more definitely modified into a “lower lip.”

When we turn from the biting insects to the haustellate or sucking groups, we find that the mouth-parts are modified in ways the most diverse for feeding on liquids. The mandibles may disappear or be reduced to minute vestiges, as in the Trichoptera, Lepidoptera, and many Diptera, or they may persist, modified into sharp piercers as in the Thysanoptera, Hemiptera, and many other Diptera. The maxillae may also be transformed into piercing organs as in Hemiptera and biting Diptera, or become modified into flexible grooved structures acting jointly as the sucking tube which is the feeding organ of the Lepidoptera. Among the Diptera the act of suction is performed by the tip of the labium, and the same function is so carried out by the Hymenoptera, an order within which the jaws of the primitive sawflies are essentially of the mandibulate type, while among the highly specialised bees the conjoined elongate and flexible inner lobes of the labium form a most beautifully perfect sucking trunk. All these facts combine to demonstrate that the arrangements of the jaws for sucking which characterise various orders of insects are not only most diverse, but have been independently acquired as modifications, often extreme, from the primitive biting type of insect mouth.

The wings of insects of different orders also show evidence of modification. Those groups such as Isoptera, Odonata, and some Neuroptera in which the hindwings and forewings are closely alike, represent generally the primitive undifferentiated condition of insect wings, but it is established by the researches of J. H. Comstock (1918) and others that among such living insects as the Isoptera, whose hindwings resemble the forewings most nearly in shape and neurulation (Fig. 64, *b*), this condition is to be regarded as a secondary reversion. Comparison of insect

wings suggests that early in the history of the class arose a general tendency of hindwings to become broader than forewings, with the development in many groups of a folding anal area; this is well seen in Orthoptera, Plecoptera, Trichoptera, and many Lepidoptera, the forewings tending to become elongate and relatively narrow. In the Orthoptera and many Hemiptera the forewings are firmer in texture than the hindwings, for which, in the resting position, they form protective sheaths. This tendency is carried to its extreme in the Coleoptera, most of whose families have the forewings (elytra) hard and horny like the body-sclerites, and devoid of all trace of the typical wing-neuration. The varying relations of the different orders in which these wing modifications are displayed suggests that they have arisen independently along several lines of evolution in the history of insects, and this view receives confirmation from the differences observable in the detailed structure of the wings themselves. In the Orthoptera the forewing is elongate, narrow and firm in texture, but it displays the typical series of nervures. This is also the case in some Hemiptera, but in the large sub-order of the Heteroptera the forewing is, as a rule, sharply divided into a larger basal and median area, which is firm and horny and shows the course of a few only of the nervures, and a smaller apical membranous area often traversed by the full series of nervures with their characteristic branches. In the beetles, or Coleoptera, as already mentioned, the hardened forewings retain no trace of the nervures ordinarily characteristic of insect wings, so that it has been doubted if they should be regarded as wings at all, and a suggestion was at one time put forward that they correspond to the tegulae. But the demonstration in the elytra of beetle pupae of the typical tracheation that prefigures the wing-nervures has established beyond doubt that these structures are indeed greatly modified forewings, and some recent discoveries among fossil insects, to be mentioned later in this chapter, throw light on the course of their modification.

The scheme of insect classification reminds the student

that not only in the organs of feeding and locomotion, but in the ways of their development and growth have insects as a class undergone much change in the course of ages, even as most individual insects undergo profound changes in their usually brief lives. Among the Apterygota the young resemble generally their parents and live under the same conditions; there is no marked transformation in the life-history. The same absence of any marked change of form is an obvious character in many orders of the Exopterygota—the Dermaptera, Orthoptera, Isoptera, Mallophaga, Anoplura, and many Hemiptera. Such “ametabolous” condition, as we have seen, must be regarded as a primitive character among insects. In certain families of Hemiptera, such as the Cicadidae and the Coccidae, the young differ markedly from their parents, and may be described as larvae, and these passing through an “incomplete” transformation are often described as “hemimetabolous.” In many of them, as among the Thysanoptera, the insect is predominantly passive before its final moult. These facts combine to emphasise a divergence between the adult and immature stages, derived from a primitive condition in which both are alike. This interpretation by increasing divergence is especially suggested by the life-history of the three orders Plecoptera, Ephemeroptera, and Odonata, whose members, aerial when adult, have a long larval life under water. In the Plecoptera, the young aquatic stonefly-grub is not unlike its parent. Differing from the latter in its place of abode, it does not differ markedly in form, though it has special thoracic gills for breathing the dissolved air. Among the Odonata there is much greater divergence, and some of the specialisations of dragon-fly larvae have already been mentioned (pp. 44, 277, 313). While the transformation of the labium into the specialised hinged and hooked “mask,” which enables the lurking larva to stalk its prey, is common to the whole order, the adaptations for breathing dissolved air differ markedly in the two sub-orders of dragon-flies. It may be inferred from this that the divergence in jaw-



structure which enables the larvae to feed is earlier and more fundamental than those modifications for aquatic life which differ within the limits of the order. From his study of the air-tube system of dragon-fly larvae Tillyard (1917) concludes that the immature stages of primitive Odonata were dwellers "in damp earth rather than in water." It is likely that the forerunners of many other insect larvae, now specialised for an aquatic life, passed ages ago through a similar "halfway house."

The Ephemeroptera (mayflies) are of great interest from the view-point of this discussion, because in them the divergence between larva and imago reaches its greatest extent among all the Exopterygota. The delicate short-lived flies have vestigial jaws, so that they take no food after acquiring their wings, of which the front pair are far larger than the hinder. While their jaws and wings thus show wide departure from the condition which must be regarded as primitive among insects, they retain the far-off ancestral character of paired openings to the genital ducts, which in all other winged insects open into a single terminal passage. They also present the archaic character of long, jointed cercopods. Their aquatic larvae, as previously pointed out (p. 185), are essentially thysanuroid insects modified for life in the water, as they agree with the Apterygota in possessing mandibles of the crustacean type; their long feelers and cercopods recall those of typical bristle-tails, and their series of paired abdominal tracheal gills are the appendages of that region modified in correspondence with life under water. They are therefore the one order of winged insects which clearly show a special relationship to the Apterygota, and their larvae, if divested of their special aquatic adaptations, may be reckoned as furnishing some indication of the wingless stock whence the earliest winged insects were derived. It will be remembered that at the close of their transformations, mayflies afford an example through the sub-imago, unknown in any other order, of a moult after acquiring the power of flight. This was probably a common condition among the primitive winged

insects, and as the sub-imago of a mayfly is the penultimate instar it corresponds with the pupa in the great metamorphic orders, though its comparatively active habits offer a strong contrast to the mainly passive behaviour of the latter.

The pre-pupal and pupal periods in the life-history of those insects that undergo a "complete" transformation (metamorphic or "holometabolous" insects) allow, as we have seen (pp. 173-6), opportunity for the extensive reconstruction necessary for the development of the winged imago from a larva that diverges widely from it in details of form and manner of life. The degree of divergence between larva and imago may be taken generally as a measure of the degree of specialisation attained by the various orders of the Endopterygota, and this divergence is often clearly very great in those orders whose members show the highest specialisation of structure in the adult. For example, the Diptera with their elaborate sucking jaws, their concentrated body-form, and the remarkable reduction of their hindwings, the forewings alone being used in flight, are developed from legless grubs or headless maggots, in many respects degraded yet often remarkably adapted for special methods of feeding. The higher Hymenoptera, which also show great modification in their body-structure, wings, and suctorial labium, offer in their adult condition a striking contrast to the small-headed, soft-coated larvae which seem so sluggish and inactive because the nursing activities of their mother or elder sisters have provided for them an abundant and appropriate food supply. The active, armoured "thysanuriform" larva, characteristic of many families of beetles and Neuroptera, is clearly much closer than the fly-maggot or the bee-grub to the primitive insectan type. All the thysanuriform larvae among the Endopterygota, however, are without abdominal appendages; these may be represented in a greatly modified form by the pro-legs of caterpillars, especially those of the scorpion-flies (Mecoptera, Fig. 78) and of the most primitive of the Lepidoptera (Micropterygidae) in whose larvae the pro-legs are im-

perfectly jointed and clawed, suggesting a correspondence with thoracic legs.

We have concluded that among the Endopterygota, as among the Exopterygota, the mandibulate orders are more

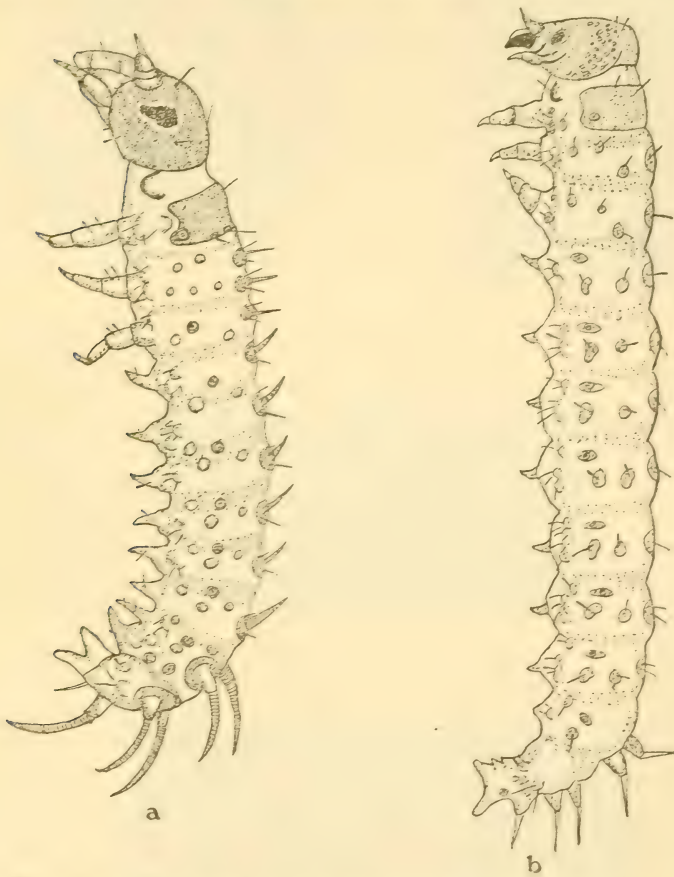


FIG. 78.—*a*, First-stage Larva of Scorpion-fly (*Panorpa klugi*) Japan (side-view),  $\times 30$ . *b*, full-grown larva (side view),  $\times 6$ . After T. Miyake (*Univ. Tokyo Coll. Agr. Journ.* iv, 1912).

primitive than those which take food by suction. The Mecoptera and Neuroptera have typical biting jaws, while among the Trichoptera and the vast majority of the

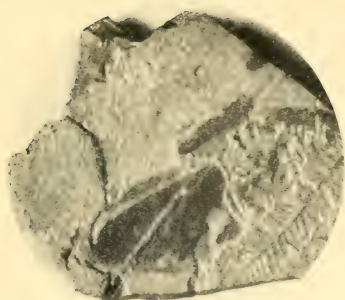


Lepidoptera, mandibles are absent or vestigial in the adult. It is interesting to notice that the caddis-flies (Trichoptera) which have no mandibles when adult, retain these jaws in the pupa which has to bite its way out of the protective "house" formed by the larva and contracted and closed before pupation. In the great majority of the Lepidoptera the pupa is without mandibles, but in those primitive Micropterygidae mentioned above, the pupa has relatively large mandibles, and these jaws are recognisable in a reduced form in the imago. The conditions in these orders suggest, therefore, a development of the more highly organised Lepidoptera from an ancestral stock some characteristics of which are preserved in the Mecoptera, Neuroptera, and Trichoptera.

That wing-structure is an important guide to the student who endeavours to trace out the relationships between various groups of insects was apprehended by the naturalists who gave more than a century ago to most of the insect orders names suggested by the nature of their wings (Coleoptera, "sheath-winged"; Lepidoptera, "scale-winged," etc.). We have seen how, in the course of a winged insect's development, air-tubes grow into its wing-rudiments, and prefigure the course of the longitudinal series of supporting wing-nervures—sub-costal, radial, median, cubital, and anal. The work of various students, notably of J. H. Comstock (1918) and R. J. Tillyard (1919), in correlating these wing-nervures in the various orders of insects has emphasised the importance of wing-neuration as a guide to the relationship. In this way a true kinship has been shown to exist between the great majority of the metamorphic orders—the Neuroptera, Mecoptera, Trichoptera, Lepidoptera, and Diptera—an assemblage which together with certain extinct orders has been distinguished by Tillyard (1918-20) as the "Panorpoid Complex."

Some evidence as to the course of evolution of the insect orders afforded by the study of fossils may now be considered. The remains of the oldest insects known to us are of Carboniferous (late Palaeozoic) Age; a number of

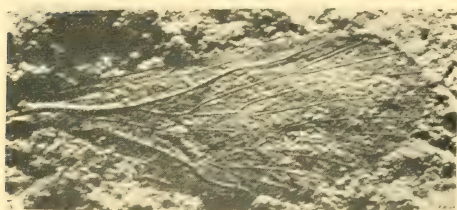
# PLATE XII



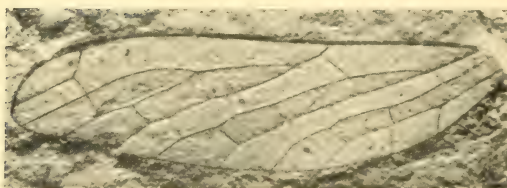
A



B



C



D

FOSSIL INSECTS. A. Palaeodictyopteran (*Goldenbergia hamyi*).  $\frac{1}{3}$  size. Carboniferous of Commentry. B. Blattoid (*Necmylacrisc meunieri*) Carboniferous of Commentry. After H. Bolton. C. Mecopteran (*Permochorista sinuata*).  $\times 7$ . Upper Permian of New South Wales. D. Protohymenopteron (*Protohymen permianus*).  $\times 3$ . Lower Permian of Kansas, U.S.A. After R. J. Tillyard.

*To face p. 336.]*





types have been described by C. Brongniart (1894), A. Handlirsch (1906-8), S. H. Scudder (1890), and H. Bolton (1921-2), from European and North American localities. Most of the insects of the Primary Era thus revealed are referred to an order, Palaeodictyoptera, now altogether extinct, characterised by the close similarity of the wings of the two pairs and the presence of long, jointed tail-feelers (cerci). Some students of these insects believe that the wings were always spread out at right angles to the body as they could not be brought together over the back. The neuration was primitive, and in some forms there were small paired plates, suggesting rudimentary wings, on the prothorax as well as a series of paired lateral expansions (pleura) on the abdomen; these structures have led to speculation as to the possibility of wing development on all segments of the primitive insect's body. The Palaeodictyoptera, some members of which (*Dunbaria*) survived until the succeeding Permian Period, afford a possible origin for most of the orders of winged insects living around us to-day. It is noteworthy that in rocks of the same Carboniferous Period are preserved remains of insects with broadened hindwings and a type of neuration approaching that of cockroaches; these are referred to another extinct order, the Protorthoptera. But in Carboniferous times lived also, as we know from fossil evidence, insects (Plate XII) which were so like modern cockroaches that it is doubtful if they should not be placed in the same family. Thus we realise that cockroaches were crawling among the rank vegetation of the ancient coal-forests, and that representatives of the more primitive stocks whence they had sprung were still surviving from earlier periods of the earth's history, though as to those earlier periods there is as yet no definite evidence from fossils. The Palaeodictyoptera suggest an origin not for the Orthoptera only but for most of the exopterygote insect orders.

That the oldest winged insects must have arisen before the period of the Coal Measures is shown by the fact that contemporary with the Carboniferous Palaeodictyoptera

were precursors of the two distinctive modern orders of the Ephemeroptera (mayflies) and Odonata (dragon-flies). In both of these there is, as has been mentioned, a curious mingling of primitive with specialised characters, and though they practise the open type of wing-growth they pass through a remarkable transformation in their development from aquatic larvae. The Protephemerida differ from living mayflies in the comparatively slight differentiation of the wings of the two pairs ; the neuriation shows an approach to the mayfly type, but there is no such extreme reduction in the hindwings as is distinctive of recent Ephemeroptera. What kind of life-history the Protephemerida passed through we do not know, but it is likely that there was at least the beginning of larval adaptation to aquatic life, as in Russian rocks of the succeeding (Permian) period has been preserved a typical mayfly larva with nine pairs of abdominal gill-appendages. The lower Permian beds of Kansas, North America, preserve numerous remains of primitive mayflies. The Ephemeroptera, therefore, essentially as we know them to-day, were already well established early in the great Secondary Era of the history of life on our earth. It is interesting, however, to notice that the hindwings of mayflies were in the Jurassic Age less relatively reduced in size than those of living forms.

Turning to the evolution of dragon-flies, we find that the Protodonata of Carboniferous times were insects with the general aspect of modern dragon-flies but without the characteristic specialisation of body-structure and wing-neuriation. Some of them were of gigantic size : the huge *Meganeura*, preserved in the Commeny beds of Northern France displayed a wingspread of some two feet. In late Palaeozoic (Permian) times dragon-flies were living which can be referred to the same order (Odonata) as those around us to-day, though they were more primitive in form than members of the two modern sub-orders Zygoptera and Anisoptera ; their remains are known from the Lower Permian beds of Kansas. A special sub-order, Archizygoptera, includes the early Mesozoic genus *Protomyrme-*

leon, of which there are three known species—one from the Upper Trias of Queensland, one from the Lower Lias of Western England, and one from the Upper Lias of Northern Germany (see Tillyard, 1925). Most of the Liassic dragon-flies belong to an order Anisozygoptera of which the wing-form recalls that of the recent Anisoptera, but the neuration is less specialised. Several distinct families of Anisozygoptera are known from the Lias and a single genus (*Epiophlebia*) survives to-day in Japan and Northern India. In Jurassic rocks of later age than the Lias are preserved remains of dragon-flies approximating closely to the existing families which have come down from the late Secondary and early Tertiary times to the present day with little change in form and life-history.

The Plecoptera (Stoneflies) also had their precursors in the Palaeozoic era. Tillyard (1926) describes the members of an extinct order, *Protoperlaria*, as a “dominant type of insect” among the series of fossils lately discovered in the Lower Permian beds of Kansas in North America. “Some of these are preserved perfectly in every detail and show a very unexpected character in the presence of well-formed wing-flaps with extensive venation on the sides of the prothorax.” Such abortive winglets recall the similar structures noticed already in certain Carboniferous Palaeodictyoptera to which the ancestral stoneflies were in all probability closely related. From the Kansas Permian beds have been disinterred also remains of early members of other allied groups such as *Embiidae* and *Psocids*.

Among the Exopterygota the Hemiptera, with their jaws specialised for sucking and piercing, form a large and very distinct order. The well-known fossil insect *Eugereon*, from rocks of Permian age in Germany (Oldenburg) shows a head with apparently typical bug-like beak and piercers, while the thorax bears palaeodictyopteroid wings. It seems evident, therefore, that the precursors of the Hemiptera had undergone radical change in the structure and function of their jaws while their wings still retained primitive form and neuration. Tillyard has, however, demonstrated (1926)



the presence of four types of undoubted Hemiptera—all referable to the sub-order Homoptera—in the Lower Permian beds of Kansas, North America. In Prosbole, from the Upper Permian of Russia, there can be traced the beginning of differentiation between the corium and membrane of the forewing that characterises the Heteroptera. Our knowledge of the course of modification in the wings of the Hemiptera is mainly due to the researches of Tillyard (1918-19, 1926), who has discovered ancestral Homoptera in the Upper Permian beds of Belmont (New South Wales) and the Upper Trias of Ipswich (Queensland) in some abundance, and in the Trias, primitive Heteroptera, such as *Dunstantia*, more sparingly. From rocks of Jurassic age in Europe have been taken fossils that establish the presence of several living families of Hemiptera at that period of the world's long history.

From the above summary it will be realised that our knowledge of extinct Exopterygota supports the conclusions as to the course of their racial development that may be drawn from the comparative study of their structure and life-history. The geological history of the metamorphic insects (Endopterygota) now calls for attention.

The combination of mandibulate jaws with four similar membranous wings with predominantly longitudinal neuration marks the Mecoptera as the most primitive living representatives of the sub-class. Tillyard has lately (1926) pointed out that the North American fossil *Metro-pator* described by A. Handlirsch (1906) from the Upper Carboniferous of Pennsylvania, "one of the eight oldest insect wings yet discovered," must have belonged to a Mecopteran. He has also described (1926) Mecoptera from the Lower Permian of Kansas; belonging to extinct families near those represented (Plate XII, C) in the Upper Permian of New South Wales and allied to the Choristidae which survive as members of the modern Australian fauna. Contemporary with these Australian Permian Mecoptera lived *Belmontia*, represented by fossil remains found at

Belmont, New South Wales, and other insects relegated by Tillyard to an extinct order Paramecoptera, "evidently representing the common ancestors at that period of the three orders Diptera, Trichoptera, and Lepidoptera." While there is as yet no definite fossil evidence of the existence of Trichoptera until the Necrotauliidae from English and European deposits of Liassic age, comparative study leaves little room for doubt that the Trichoptera arose in Triassic times as a primitive side branch from the stem that developed into the great order Lepidoptera; the statement often made that caddis-flies are directly ancestral to moths and butterflies is misleadingly simple. The "record of the rocks" is disappointingly incomplete with regard to the history of the Lepidoptera; apart from problematic remains of Jurassic age there are no fossil Lepidoptera until the Tertiary (Cainozoic) era is reached; then in the well-known Miocene beds of Florissant in Colorado and Oeningen in Baden, occur a variety of Lepidoptera belonging to existing families. From comparison of the two sub-orders of Lepidoptera it appears certain that the primitive Homoneura preceded the now dominant Heteroneura in the time of their development.

The Paramecoptera appear also to have been ancestral or approximately so to the Neuroptera. Of the two neuropteran sub-orders the Megaloptera, with their comparatively primitive larvae and simpler wing-neuration, are clearly older than the Planipennia; we find that while the former are represented by fossil wings (*Triadosialis*) from the Lower Trias of Germany, the latter have no known representatives until *Archeopsychops* and its allies from the Upper Trias of Queensland. There are still very great gaps in our knowledge of these fossil insects; when we remember the delicacy of their build and the improbability of their preservation in large numbers in water-formed deposits, this "imperfection of the record" is not surprising. It is all the more satisfactory that such information as we have from fossil insects confirms so definitely the conclusions drawn from a study of the structure and life-

history of the insects living around us to-day as to the general course of their evolution.

The extreme modification of the wings among the Diptera renders the order one of exceptional interest to the student of insects. The Upper Triassic beds of Queensland have yielded fossils representing four genera (*Aristopsyche* and others) which Tillyard places in a special extinct order, the Paratrachoptera, arising, as its name implies, along with the ancestral Trachoptera from the Paramecopteroid stem. These Paratrachoptera are believed by Tillyard to have been actually "ancestral to the true Diptera." All their wings that have been examined are apparently forewings, intermediate as regard venation between the Mecopteroid and Dipteran type. Tillyard is of opinion that the hindwings of these insects were not very different from the forewings; we still have no definite information how they became reduced and modified into the Dipteran halteres. The oldest known fossils referable to true Diptera are from European beds of Upper Liassic age, and these belonged to the sub-order Nematocera and to those sections of the Brachycera whose larvae (like the grubs of Nematocera) have a definite head-capsule. The earliest known members of the cyclorrhaphous Brachycera (flies whose larvae are headless maggots) are of Tertiary age, and their fossil remains come largely from the same beds as those in which the great majority of fossil Lepidoptera are preserved.

The Hymenoptera are, like the Diptera, one of the most highly specialised orders of living insects. It is therefore of great interest to find that some fossils from those Lower Permian rocks of Kansas, which have yielded so much information of the greatest importance to the student of insects, prove to represent the ancestral stock of the Hymenoptera. These wings are referred by Tillyard to an extinct order Prothymenoptera among whose members "fore and hind wings were of almost equal size and were not yet linked together in flight by hooklets." Tillyard places also among the Prothymenoptera the only Carboniferous fossil (except *Metropator* mentioned above) referable to the Endoptery-



gota ; this is Sycopteron from Commentry described by H. Bolton (1917) as a mecopteroid fly. In wing-neuration these insects show features of " the primitive mecopteroid plan " combined with " strong hymenopterous characters," such as approximation of the radial system of nervures to the costa of the wing and the consequent development of the distinctive pterostigma (Plate XII, D). From these Protohymenoptera of the Carboniferous and Permian there is a long gap in the record to the earliest known fossils that are certainly referable to the Hymenoptera. These come from the European Jurassic, and are sawfly-like insects of the sub-order Symphyta. The highly organised Hymenoptera of the sub-order Apocrita are not known to have lived before the Tertiary era ; ants and other existing families are represented in the Oligocene amber of the Baltic as well as in the Miocene rocks of Colorado and Germany. We realise, therefore, that the geological history of the Hymenoptera, so far as we know it, supports the conclusions drawn from the comparative study of living members of the order. It is of much interest to notice that the three groups of insects—Lepidoptera, cyclorrhaphous Diptera, and Hymenoptera Apocrita—which in their manner of life and ways of feeding are so closely dependent on the higher flowering plants, attained their full development at that period in the course of the earth's history which is distinguished by the dominance of the section of the Vegetable Kingdom wherewith their lives are so closely bound up.

The mecopteroid features of the wings of the Protohymenoptera suggest that they, like the Paramecoptera, had a common origin with the primitive scorpion-flies during or before the Carboniferous Age. Tillyard, however, in a recent discussion (1926) on these extinct orders of insects, expresses the opinion " that there were three distinct groups of holometabolous insects which evolved a pupal stage independently of one another early in the Permian Period," and that the Hymenopteroid stock had an origin apart from the great assemblage of orders (Mecoptera, Neuroptera, Trichoptera, Lepidoptera, Diptera) that make up the

“Panorpoid Complex.” It is certain that the inter-relationship of these orders is closer than their kinship to the Hymenoptera, and that for a common origin we must certainly go back to the Carboniferous Period ; but stronger evidence is required than any yet available to establish the independent origin of “complete” metamorphosis in two of these ancient insect groups. A common, if far off, ancestry for the Hymenoptera and the Lepidoptera is suggested by the close resemblance shown in the arrangement of the bristle-bearing tubercles on the body-segments of the larvae in the two orders. Such a detail of structure as this is stronger evidence of relationship than the outward similarity in the caterpillar type of larva common to moths and sawflies, which may probably be due to adaptation to similar conditions of life.

There remains only one large order of the Endopterygota to be considered in this survey of relationships—the Coleoptera or beetles, which with their biting jaws and forewings modified into firm sheaths (elytra) form one of the most distinct and characteristic of all the orders of insects. Geologically, beetles are of considerable antiquity, far older than the Diptera, Lepidoptera, or higher Hymenoptera, as fossils referable to existing families have been found in the early Secondary (Triassic) rocks of Europe, including weevils (Curculionidae) and leaf-beetles (Chrysomelidae) both specialised groups. Among the fossil insects of the Upper Trias of Queensland lately studied by Tillyard, “Coleoptera are dominant, making 46 per cent. of the total fauna.” Many of these belong to the Hydrophilidae. Beetles are also represented, though much more sparingly, in the older Upper Permian rocks of New South Wales ; and in these deposits Tillyard has discovered along with the beetles, “a most remarkable series of larger forewings evidently allied to them and showing all gradations from a flattened, apically pointed tegmen with complete venation down to half-formed elytra with the venation completely lost except in the anal region. These must be regarded as being remnants of the older order from which the true

Coleoptera originated, and are called Protocoleoptera." From this highly interesting discovery it is clear that the specialised sheathing forewings (elytra) of beetles were modified from somewhat firm forewings (tegmina) resembling those of the Orthoptera and many Hemiptera, and this modification must have been at least begun in Carboniferous times. Possibly other early fossil forms yet to be unearthed, will make it clear that the specialised neurulation of the Protocoleoptera can be derived from that of the most primitive Mecopteroid insects. If so we shall be convinced that all the Endopterygota are related among themselves and form a truly "natural" group, a conclusion that seems justified in view of their distinctive common type of life-history. Tillyard (1926) inclines, however, to the view that the beetles originated from some exopterygote group independently of the other orders which undergo complete transformation.

The facts summarised in the preceding pages are enough to convince us that notwithstanding many considerable gaps in the geological record of the insect life of the past, there has been from the Carboniferous to the Recent Period general progress from the simpler to the more specialised types of structure and life-history within the class. We realise that the various forms of larvae adapted to particular modes of life have arisen by divergence, often clearly degenerative, from the adult forms as these became more highly elaborated. Nor must it be forgotten that the existence of groups of wingless insects related to winged orders, tells of degeneration as well as progress in the evolutionary history of the race. The greatest gap in our knowledge of this subject is evident when we think about the origin of insects' wings. As the oldest fossil insects known all possessed the power of flight, there is no definite evidence how the primitive Exopterygota acquired their wings. In the stages of development in the individual insect the wings grow out from the tergal region of the thoracic segments as hollow, flattened pouches; this fact indicates the morphological nature of the wing, but it



throws us back on surmise as to how, in the course of racial history, the wing as an organ of flight was developed out of a thoracic outgrowth less than a wing, such, for example, as the prothoracic "winglets" of some Palaeodictyopteran. Two surmises may be mentioned. C. Gegenbaur (1871) suggested that wings are modified tracheal gills, indicating an originally aquatic manner of life among primitive insects; this view is inadmissible because the typical insectan air-tube system is adapted for atmospheric breathing and all branchial modifications are clearly secondary. A. S. Packard (1898), G. C. Crampton (1916), and others have supposed that the thoracic outgrowths, early in the history of primitive insects, were of service as parachutes and that a capacity for gliding motion preceded the power of true flight. It may have been so, but the subject is one as to which it is wise to admit ignorance. The problem how wings arose in the course of racial history is one of those problems of evolutionary adaptation which involves some of the questions of method to be discussed in the remainder of the chapter.

The class of Insects belongs, as we have seen (Chap. I, p. 2), to the great phylum of the Arthropoda, and a discussion of the course of insect evolution would be incomplete without some reference to the relationship of insects to other classes of that phylum. As this question is mainly morphological it cannot be treated in detail in the present volume. It is clear, however, that apart from their distinctive power of flight, insects are adapted for their life relations—feeding, sensation, response, movement—in essentially the same way as are members of the other arthropodous classes. More than once (see J. S. Kingsley, 1894, and A. S. Packard, 1898) the suggestion has been made that the Arthropoda should not be considered a natural group, but regarded as an assemblage of classes which originated independently of each other from segmented worms (Annelida). The distinctive features of the Arthropoda are, however, too characteristic and remarkable to be explicable as the result of convergence, as E. R.

Lankester (1904) has convincingly demonstrated. The abdominal limbs of *Thysanura* (Fig. 52, B) and the rudiments

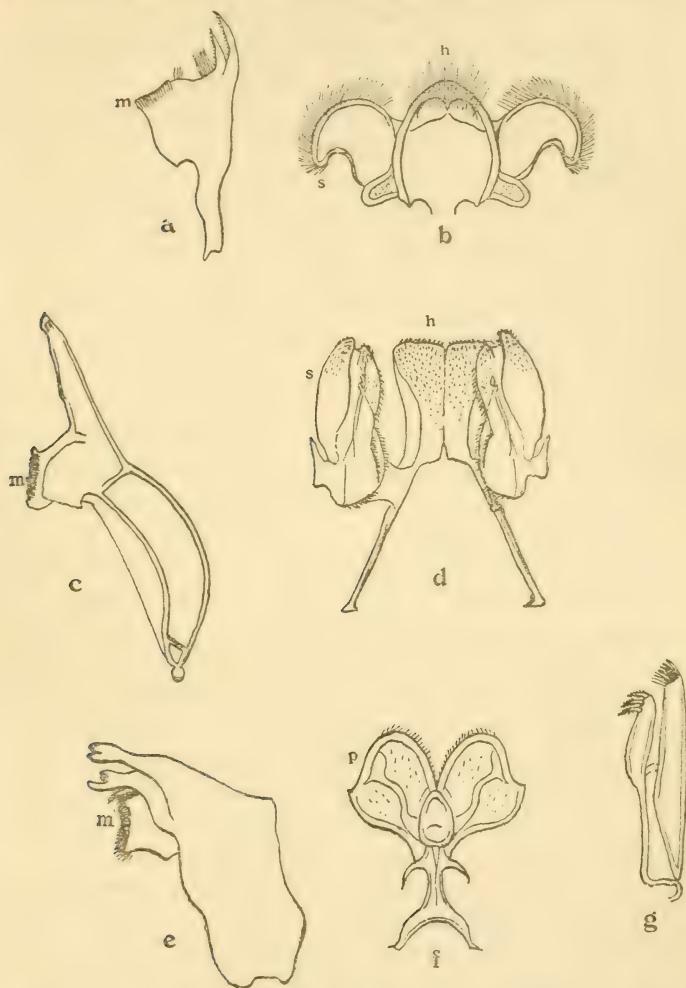


FIG. 79.—*a*, mandible (*m*, molar area); *b*, hypopharynx (*h*) and superlinguae (*s*) of Mayfly Larva (*Heptagenia*).  $\times 12$ . After Vayssi re (*Ann. Sci. Nat. Zool.* xiii. 1882). *c*, mandible; *d*, hypopharynx and superlinguae (the left superlingua displaced) of Bristle-tail (*Petrobius*).  $\times 30$ . *e*, mandible; *f*, hypopharynx and paragnaths (*p*); and *g*, maxillula of Isopod Crustacean (*Ligia*).  $\times 12$ . After G. O. Sars (*Crustacea of Norway*, ii, 1899).

of those appendages which can be seen on the embryonic segments (Fig. 40, C) of many insects before hatching, suggest that the ancestors of insects had paired limbs on all or most of their segments, a condition persisting in the Chilopoda (centipedes), Diplopoda (millipedes), Symphyla, Crustacea, and in the aquatic Arachnida (the living horse-shoe "crabs," *Limulus*, and the extinct Eurypterids). In all classes of the Arthropoda a definite head consisting of five or six limb-bearing segments is evident, except among the Arachnida and those Crustacea in which this region is fused with the segments behind it to form a cephalothorax. The relationship of primitive Insects to Crustacea is clearly shown by the similarity of the compound eyes in the two classes, by the close likeness of the mandibles of Thysanura and larval mayflies to those of various Crustacea (Fig. 79, *a, c, e*), and by the presence in those and other adult and larval insects of a pair of probably appendicular lobes in front of the tongue, which represent either the crustacean paragnaths or maxillulae (Fig. 79, *f, g*). These evidences of kinship between insects and crustaceans have been strongly emphasized, though with differences of opinion as to details, by H. J. Hansen (1893), and C. Börner (1909), and G. C. Crampton (1921) as well as by the writer of this book (Carpenter, 1903, 1905, 1924). To the points already mentioned may be added the striking fact that in the Insecta, Arachnida, and malacostracous Crustacea, as well as in the small but highly interesting class of the Symphyla (whose members combine characters of insects, centipedes, and millipedes) there appears to be precisely the same number of segments in the body. Such close numerical correspondence cannot be a mere coincidence; it must indicate relationship, and it is interesting to note that T. H. Huxley nearly seventy years ago (1859) commented on the great significance of a cockroach, a lobster, and a scorpion possessing exactly the same number of somites. We must await further palaeontological evidence before offering any definite opinion as to the group of Crustacea to which insects may be most



nearly related. Handlirsch has emphasised supposed points of correspondence between the Palaeodictyoptera and the Trilobites—that extinct crustacean group so characteristic of the Palaeozoic seas. Hansen and Lankester have, with more reason, pointed out the close correspondence of the head and its appendages in primitive insects and in the Isopoda, a crustacean order which can be traced back to Devonian times and which has given rise to air-breathing forms like the woodlice. The generally acknowledged relationship of Insects to the Centipedes and the Symphyla leads us, however, to doubt if they can have specially close affinity with so highly organised a crustacean order as the Isopoda. It seems likely that in the origin of insects, in early Palaeozoic times from their primaeval stock, the restriction of their important locomotor limbs to the six thoracic legs must have been a dominant factor in their differentiation as it certainly has been in the subsequent course of their evolution.

We turn now to consider a large subject which has given, and still gives, occasion for much controversy: the method of evolution in the insect world. This is clearly part of the still larger question of the method of animal evolution generally; its discussion in a book on the Biology of Insects is appropriate because many lines of inquiry pursued by students of these creatures are found to shed light on those problems of inheritance and development which the student of animal life in its widest aspect seeks to solve.

The summary of the probable course of insect evolution given in the preceding pages clearly implies the belief that there is a true relationship between the various groups of insects living around us in the world to-day, that these are the descendants of the insects of past ages of the earth's history, and that as the living groups differ in various degrees from one another and from their extinct ancestors, there has been through the long periods of geological time a process of "descent with modification," a phrase that has often been used to explain and define in brief the modern

naturalist's principle of organic evolution. The conception of descent with modification inevitably recalls the subject treated in Chapter VI. of this book, the great subject of Heredity, from the study of which it is realised how through the definite yet unknown factors lodged in the germ-cells, characters are inherited and transmitted through successive generations. Heredity has often been expounded by the expression "like begets like" or "the offspring resembles the parent." But the facts of inheritance, as shown by the moths and fruit-flies mentioned in that chapter (pp. 121-131), convince us that these expressions need qualification. The likeness of offspring to parent is not absolute, members of the same family may differ in various details from either parent or from both as well as among themselves. Observation and experimental breeding among insects as among other creatures, convince the student that Heredity may involve Variation, and that these are not, as is often imagined, antagonistic, because the variation which distinguishes a member of some family from its parent or brother is due to a definite factor in a germ-cell borne in that parent's body. Every inherited variation that appears depends on the nature of the "physical basis of heredity" in the egg, fertilised or unfertilised, whence the creature which shows that variation has developed. Therefore, since by evolution we understand descent with modification, it follows that in studying heredity with variation we are face to face with the basal or primary factor of the process.

The increasingly divergent groups of the systematic zoologist: variety, species, genus, family, order, class (with the intermediate "sub-" and "super-" groups), suggest that the wider differences, such as those of genus and family, are extensions of the smaller differences such as those of variety and species. Thus we are again brought to the conclusion that in the observable variation, within the limits of a species, which is often an accompaniment of the inheritance of ancestral characters, we see, as it were, the raw material for the evolutionary process. The detailed and critical study of variation during the last twenty-five

years owes much to the work of W. Bateson (1894), and it is evident that such study is greatly simplified in cases where the variation is discontinuous, that is, where some one or more clear-cut distinctions between "variety" and "type" can be definitely shown, as in the blackish scaling of the wings of the *doubledayaria* form of the moth *Amphidasys betularia*, or in the white-eyed offspring of normally red-eyed fruit-flies (*Drosophila*). These are examples of the alternative characters specially suited for the investigation of heredity on the principles of Mendel (pp. 121-131). Now, in the case of some distinctions of this nature there are records of the occurrence of both forms as far back as the species have been studied by naturalists, so that the appearance of one or the other is due to the sorting out in the maturation of the germ-cells of factors that have been handed down for a long series of generations. In other cases, however, including those of *Amphidasys* and *Drosophila*, just mentioned, the dark scaling of the former and the white eyes of the latter appeared at a definite recorded time in the history of the race; in the case of *Amphidasys betularia* the new dark-winged variety *doubledayaria* was observed rather rapidly to replace the light-winged type over considerable areas over northern England. Here, then, is seen a definite example of the appearance and establishment of a new form of insect. During recent years, since attention has been directed by Bateson and others to the importance of discontinuous variation, and especially since the promulgation of the Mutation Theory of H. de Vries (1901-3) founded on the apparently sudden appearance of new varieties of plants, many students of the subject have attributed a leading part in the evolutionary process to such mutants as are exemplified by the *doubledayaria* race of *Amphidasys betularia* and the white-eyed and short-winged forms of *Drosophila*. The immediate cause of these mutants is to be sought in the origin of some new factor in the germ-plasm, but there is little beyond speculation to suggest how such new factors arise, or even what they are. We know from many carefully conducted breeding experiments that changes in the germ-



plasm must continually occur, and there is little doubt that these are modifications of chemical constitution and shifting of the position of particles in the chromosomes. It is evident also that if these changes in the germ-plasm become apparent in the characters of the organism that is developed from the egg, there must be some arrangement for passing on to the cell-substance the effect induced by the germinal modification. "That which is conferred in variation," suggests W. Bateson (1914), "must rather itself be a change not of material but of arrangement or of motion." It is well known to students of inheritance on Mendelian lines that factors for apparently new characters may become apparent through the "release" of factors in the germ-plasm, owing to the elimination of other germinal factors which act as inhibitors. This mode of germinal working has led Bateson to the conclusion that "variation both by loss of factors and by fractionation of factors is a genuine phenomenon of contemporary nature," and from this starting-point to suggest that "we must begin seriously to consider whether the course of evolution can at all reasonably be represented as an unpacking of an original complex which contained within itself the whole range of diversity which living things present." With regard to the moth *Amphidasys betularia*, mentioned above, Bateson comments: "Though at first sight it seems that the black must have been something added, we can without absurdity suggest that the normal is the term in which two doses of inhibitor are present and that in the absence of one of them the black appears." From many points of view such a speculation is fascinating and alluring; it is not easy, however, to accept the conclusion that increasing complexity of structure and perfection of behaviour in the developed creature has been brought about not through elaboration but through progressive simplification of the germ-plasm. We should indeed regard with wonder the primitive thysanuriform insects of the early Palaeozoic periods, if we could believe that in their germ-cells, veiled as yet by numberless inhibitors, there were lying latent

factors destined to produce in due time the gorgeous wing-colours of tropical butterflies, the profound transformation shown in the life-history of a bluebottle, and the complex co-ordinated activities displayed in a community of ants or honey bees. It is interesting to notice that the conception of such a predetermined evolution offers a parallel to the old theory of an "evolutio" in individual development, according to which the form and characters of the adult were present, wrapped up as it were in the germ and needing only to be unfolded in the course of growth. It is hardly necessary to point out that observation of the facts of development long ago established the truth of the opposite theory of "epigenesis," the building up of the specialised organs and tissues by progressive differentiation from those primitive cell-layers which result from the segmentation of the egg.

Students of variation among animals commonly contrast with the discontinuous variations or mutants which we have been considering, those continuous variations or fluctuations which seem to merge gradually into one another when large series of specimens of the same species of creature are compared. This type of variation appears to be well demonstrated in the wing-patterns of many Lepidoptera. If, for example, a representative collection of British owl-moths (Noctuidae) be examined a species such as *Agrotis lunigera* or *Xylophasia monoglypha* is found to comprise a graded set of insects whose forewings vary from a lightish grey or reddish to an almost black shade. In the smaller common *Miana strigilis* belonging to the same family, there are typically present on the grey forewing pale markings outlining the characteristic dark dots (stigmata) on the disk of the wing and forming a conspicuous postmedian transverse band. Through an increasing development of dusky scaling over the surface of the wing, a condition is reached in which the whole area appears almost uniformly dark and the pale markings absent. Our well-known Peacock Butterfly (*Vanessa io*) is distinguished by the presence of handsome "eye-spots" on both fore and hind wings, the

latter being almost circular black areas, each enclosing patches of blue or purple and surrounded by a broadish yellow border, while the "eye-spots" in the forewings are less definite, the inner boundary of each being yellowish while the outer is formed by a series of yellowish, blue, and lilac spots or patches, which represent the set of white spots that are conspicuous in allied species at the same region of the forewing. The central area of the forewing eye-spot in *V. io* is partly of the blood-red hue of the general wing-area suffused with black scaling. From the typical form in which this black scaling is dense, and the rounded outline of the forewing eye-spot well marked, a series can be traced through which the black scaling fades away and the outer pale patches becoming feebler, the characteristic forewing eye-spot is no longer distinguishable—the variety *fischeri* of M. Standfuss (1896).

It is important, however, in the study of variation to remember that continuity cannot be inferred simply from arranging a graded series among specimens collected haphazard from various localities. A frequency of the various forms in relation to the general population, so that the extremes tail off from a "modal" form corresponding more or less closely to the mean value of the character under consideration is a condition necessary to establish the case as one of continuous variation, and this is more readily tested where some quantitative feature, such as the size of the whole insect or the proportionate size of some part of its body to the whole, is under observation rather than such a feature as colour pattern. A well-known and very instructive investigation on these lines was made on a large number of male earwigs all collected on the Farne Islands off the coast of Northumberland and described by Bateson (1894). The forceps of male earwigs are longer than those of females and more strongly curved, their length varying to such a degree that the existence of two or three different species has been imagined from this character. In the specimens examined the actual length of the forceps varied from 2 mm. to 9 mm., and a series could be arranged



showing a gradual transition from one extreme to the other. When, however, the numbers of the individuals with forceps of the varying lengths were plotted, a graph was obtained demonstrating that the whole population was grouped around two modal values of respectively 3.5 mm. and 7 mm. in length of forceps. The insects, except for the exceedingly small number that showed a forceps length of 4.5 mm., were in fact separable into a "low" and a "high" group.

The examples that have been given may suffice to show that discrimination between continuous and discontinuous variation must often be difficult. Since the work of Bateson there has been an increasing tendency among students of the subject to lay stress on the importance of discontinuous variations or mutants as the starting-point for further evolutionary progress in the origin of a new species. It will be remembered that many of the observed mutants are distinguished by characters whose factors are segregated in inheritance, and therefore remain stable; and it is stability, the tendency to breed true, rather than an extensive divergence from the type, that distinguishes a mutant from a mere fluctuation. Hence it is usually necessary, in order to discriminate between types of variation, to carry out observations and experiments in breeding. Even when a continuously graded series of varieties within a species can be demonstrated, it does not follow that such a series represents successive steps in the variation. The fruit-flies (*Drosophila*), so well known now as subjects for the study of heredity, have normally winged individuals and others with the wings more or less reduced so that they may become degenerated to the merest vestiges. These last arise as the offspring of normal winged parents, not as the final result of a series of generations showing a slowly progressive degeneration of the wings. The modern study of variation has at least demonstrated that in a single generation a marked and definite change may in many cases be observed.

A suggestive example of some of the questions concerned with variation is afforded by the small European butterfly

*Polyommatus astrarche* (now sometimes known as *Aricia medon*), which is a common insect in most parts of England. Though a member of the Lycaenidae, or family of the "Blues," it has no obvious blue scaling on the wings, which are blackish-brown above with a terminal row of orange-red spots, and greyish below with a set of the black white-ringed eye-spots characteristic of the "blue" group. In Scotland this typical form of *astrarche* is replaced by the variety or sub-species *artaxerxes* in which the terminal row of orange spots are faint in the female and wanting in the male, while the forewing shows a central white spot above, and all the spots beneath the wings are entirely white showing no black centres (Plate XIII). Along the coastal region of Northumberland and Durham the ranges of the two forms overlap, and here may be found intermediate phases, several of which have received distinct varietal names. The true connection between these different forms has long been a subject of discussion among students of insects. A study of the "mixed population" of these butterflies in the north-east of England might suggest a case of continuous variation. After careful study of the subject J. W. H. Harrison and W. Carter (1924) have given good reason for concluding that *artaxerxes* arose as a mutation from *astrarche*; the two forms breed true and *artaxerxes* is found nowhere but in northern Britain and western Ireland, while *astrarche* ranges right across the Euro-Asiatic continent. The mixed assemblage of intermediate phases of the insect found in Northumberland and Durham is due to mixed breeding, which indicates Mendelian inheritance because segregation of the parent races occurs, since "pure *medon* and *artaxerxes* are to be taken constantly and in goodly numbers." Complete geographical isolation of the *artaxerxes* race or its infertility with *astrarche* would result in definite specific distinction.

The appearance of a stable variety or mutant which may form the material for a new species is due, as we have seen, to a change within the germ-cells whence the creature develops, but as to the nature and origin of such germinal

# PLATE XIII



A. *Polyommatus astrarche* (females) right, and var. *artaxerxes* (male and two females) left.



B. *Selenia bilunaria*, male and female.  $\times 1\frac{1}{2}$ .

To face p. 356.]

[H. Britten, photo.]





change we have no definite knowledge. In many cases it must be due to internal processes about which it is hardly possible even to guess; but the question is being continually asked whether changes in the germ-plasm can or cannot be induced by changes in the surroundings and conditions of life of the animal within whose body the germs are developed and sheltered. Here we are faced with a possible factor of evolution as to which the greatest controversy has prevailed—the influence of the environment and the activities of the individual organism on the progress of the race to which it belongs. There is no doubt whatever that an individual insect is itself affected by what it does and experiences. The course of development, both before and after hatching, although it depends on the inherited constitution of the embryo or larva, requires a definite and suitable environment if it is to be worked out to its normal close, so that the young may attain maturity and in turn leave offspring to carry on the race. The question at issue, however, is whether the inherited nature of succeeding generations can be affected by the conditions of the nurture (in a wide sense) to which individuals of the parent generation may be subjected. If this question be answered affirmatively, it may be assumed that in a series of generations subject to the same influences there will be a cumulative effect on the inherited characters, and as a result the possibility of progressive change.

The importance of this factor in evolution (it is now conveniently known as the factor of “use-inheritance”) was strongly advocated more than a century ago by the famous French naturalist J. B. de Lamarck (1809), who endeavoured to prove that the racial development of the whole animal kingdom was due to “acquired changes.” He observed that “the environment affects the shape and organisation of animals,” and influences their activities and habits; and from these premises—true to some extent at least—he inferred that the changes thus impressed upon the individual must become part of the racial inheritance. “The frequent use of any organ . . . leads to its development

and endows it with a size and power which it does not possess in animals which exercise it less." The opposite result is also assumed: "The permanent disuse of an organ, arising from a change of habits, causes a gradual shrinkage and ultimately the disappearance and even extinction of that organ." And the modification thus acquired is believed to be transmitted to the race: "All the acquisitions and losses wrought by nature on individuals . . . are preserved by reproduction to the new individuals which arise." Among the examples cited by de Lamarck in support of his theory are "many insects," which, although they "should have wings according to the natural characteristics of their order . . . are more or less completely devoid of them through disuse." This is a suggestive illustration in view of the discussion earlier in this chapter (p. 346) on the origin of the wings of insects, for if use-inheritance really works it might have been a factor in elaborating these organs from some primitive rudiments which at first were less than wings. Use-inheritance as a factor of evolution has appealed to the imagination of multitudes and was accepted as a true cause by many naturalists of the nineteenth century, though they did not follow de Lamarck in regarding it as the most important agent in the evolutionary process. Because the effects of use and disuse of organs and faculties are often unmistakably apparent in the individual, it seems natural to conclude that they must also be exhibited in the history of the race. Many are thus ready to believe that among insects, the possession of ample wings follows from strenuous efforts to fly on the part of far-off ancestors, or that the blind beetles and spring-tails characteristic of a modern cave-fauna have lost the power of sight on account of the unknown number of past generations that dwelt in darkness. Such explanations involve the view that modifications during the lifetime of the individual through environment, activity, or inaction, tend to become congenital so that their effect can be traced, at least to some extent, in succeeding generations. This theory of "acquired changes" which become hereditary



means that the germ-plasm which contains the factors determining the inherited constitution of offspring and descendants is somehow affected by the experiences and actions of the creature in whose body the germ-cells are developed. Scepticism as to this influence has been increasingly dominant in the minds of those who have studied the subject since the promulgation by A. Weismann (1893) of his "germ-plasm" theory, according to which there is a cardinal distinction between the essential substance of the germ-nuclei and the nuclei of the various tissue-cells of the body ("somatic" cells), and especially since the demonstration of the great importance of the germ-nuclei in inheritance which has come through recent cytological and Mendelian research (see pp. 118-131). A detailed exposition and discussion of Weismann's theory would be out of place here, but his essential contention is that the germ-cells in each generation must be regarded as originating from the germ-cells of the preceding generation, and not from the body-cells of the creatures that carry them; hence the germ-plasm is continuous through all the generations of a race, while the bodies are evanescent. This view, though to a great extent theoretical, derives observational support from those cases in which the germ-cells of a developing animal are recognisable at a very early stage as distinct from the body-cells. The early observations of Weismann (1863) on the embryology of chironomid midges and of E. Metschnikoff (1866) on the abnormally developing virgin eggs of cecidomyid larvae, demonstrated, at the hinder pole of the segmenting egg, cells of distinct appearance; Metschnikoff and later observers traced the ova or sperms from these "pole-cells" (Fig. 80, *g*) through what is now known as a definite "germ-track." Such germinal pole-cells have now been detected in the embryos of insects of several orders besides the Diptera—Orthoptera, Coleoptera, Hymenoptera, for example; R. W. Hegner (1914), one of the recent students in this line of inquiry, has given a good general account of the distinctive granular or other inclusions in the early differentiated germ-cells, and it is

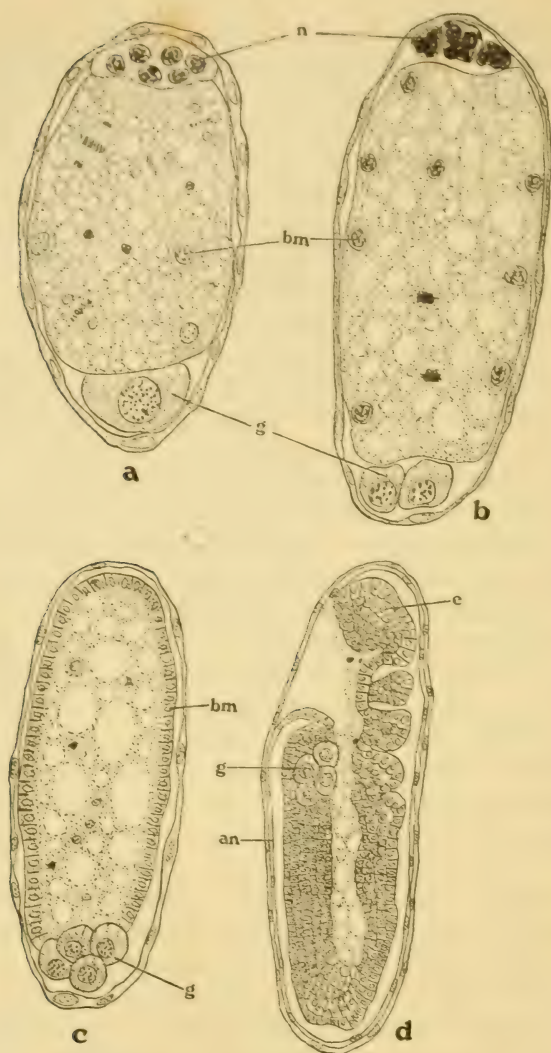


FIG. 80.—Stages in the paedogenetic development of *Miastor americana*. *a*, early stage showing a few somatic cells (*bm*), a group of nutritive cells (*n*) and one "pole" primordial germ-cell (*g*); *b*, later stage with two "pole" germ-cells (*g*), somatic cells (*bm*) toward edge of yolk; *c*, blastoderm (*bm*) enclosing yolk, and group of eight germ-cells (*g*); *d*, embryo with head-region (*e*), segmenting body, amnion (*an*) and germ-cells (*g*) at hinder end. All highly magnified. After R. W. Hegner (*Journ. Morph.* xxv, 1914).

not unreasonable to conclude that in the large number of insect embryos in which the primitive germ-cells seem to arise from ordinary mesoderm, they are really descended from certain cells which were already defined in the early segmentation stage, though showing no distinctive aspect then recognisable by the investigator. J. A. Nelson, though unable to trace early differentiation in embryos of the hive-bee (1915), believes it "probable that in all insects the germ-cells are segregated at an early period."

We have already noted that the various stages and the final result of a creature's development depend upon its surroundings as well as upon its inherited constitution. This is clearly shown by many Lepidoptera which, passing through two life-cycles in the year, appear in alternating warm or cool, wet or dry, seasonal forms. Members of the spring brood of our native common white butterflies, which emerge from wintering pupae, have their wings more darkly marked than those of the summer brood which pass through the pupal stage in June or July. These differences, brought about partly at least by the great difference in the temperature to which the pupae are subject during development, can to some extent be reproduced by artificially induced conditions. A. Weismann (1882) showed that by cooling summer pupae of the Green-veined White Butterfly (*Pieris napi*) the resulting imagos were rendered so dark that they approached in appearance the dusky arctic and alpine variety *bryoniae*. F. Merrifield (1891), by refrigerating summer pupae of the geometrid moth *Selenia*, induced such dark scaling in the resulting imagos that they resembled the strongly banded spring form of the insect. Attempts to rear the summer form of such seasonally dimorphic insects by subjecting the winter pupae to artificial heat have been only occasionally successful. In nearly all these cases it is found that the abnormal temperature-conditions must be repeated in every generation if the colour-modification is to be maintained; none of the acquired changes are as a rule inherited. What is always inherited is a power of response to the conditions that may be imposed naturally



or artificially. In the case of the Small Tortoiseshell Butterfly (*Aglais urticae*), however, it has been claimed that among a small number of insects reared at normal temperatures, the darkening that had been artificially induced in the parents reappeared to some extent in the offspring. This has been claimed as a definite case of "use-inheritance," but it may be objected that the strain of insects used in such experiments possessed an innate tendency towards darkening of wing-pattern, a suggestion evidently hard to prove or disprove. It is also said by upholders of Weismann's theory that if such effects do reappear in a second generation, the result must be attributed to the direct action of the surroundings on the germ-plasm ; but the germ-cells are during the time of action of the environmental influence within the body of the parent, and any effect on them must be in some way due to transmission of stimulation, apparently by some soluble substance, through the body-tissues.

In connection with this question the researches of W. L. Tower (1906, 1918) on colour modifications in American leaf-beetles of the genus *Leptinotarsa* are considered by many to be important though his methods have been criticised by opponents of his views. These insects are mostly yellow or brown with black markings on the prothorax and dark stripes on the wing-cases ; the patterns of the adult beetles can be modified by changed conditions of temperature and humidity during the larval and pupal stages. Tower claims that such modifications were not transmitted by inheritance if the abnormal conditions were restricted to the earlier stages of the insects' development, but that the modifications became hereditary when the abnormal conditions were continued through the maturation period ; then it is stated that the offspring of the modified beetles resembled their parents, though not subject to the same abnormal surroundings ; hence a direct action of the environment on the germ-cells may be inferred. A different interpretation is offered by B. Dürken (1923) from the result of his researches on the influence of

various types of light on the colour of the pupae of the common Large White Butterfly (*Pieris brassicae*). When caterpillars about to pupate were subject to orange and red light-rays, the black and white pigment in the underlying cuticle was much reduced in amount so that the pupa when revealed was predominantly green. Inheritance of such induced characters was established in so far as the parents had displayed them. Hence Dürken concluded that there was definite evidence of somatic influence on the germ-cells. The wing-pattern of the butterflies emerging from these modified pupae showed no deviation from the normal characters of the species.

A recent noteworthy contribution to this vexed question has been made by J. W. H. Harrison and F. C. Garrett (1926). The darkening of the wing-patterns among Lepidoptera, such as that shown by *Amphidasys betularia*, var. *doubledayaria*, is often specially noticeable in manufacturing districts, and has been attributed, in some instances, to contamination of the caterpillars' food through substances discharged into the air in those localities. Harrison and Garrett experimented with common British geometrid moths in which the dark (melanic) modification has been rarely observed, and obtained for their investigations typical pale-winged strains from the south of England. Caterpillars of *Selenia bilunaria* (Plate XIII, B) from the eggs of such moths, were divided into two sets, one fed on twigs of uncontaminated hawthorn and the other on hawthorn twigs placed in a solution of lead nitrate. All the moths of the former set were normal in their wing pattern through several generations, but in each of the two families of caterpillars fed on lead-contaminated leaves, black-winged moths appeared in the third generation—in one family a single male out of twenty-seven, in the other two out of thirty-one. In a family of the next generation, offspring of a normal pair, there were two melanic females and one male. From the small numbers and gradual appearance of the dark-winged insects, the investigators conclude that the blackening of the wings of the moths was a result of the lead salt

in the food of the caterpillars. Breeding experiments by pairing a melanic male with a normal female and feeding their caterpillars on untreated hawthorn resulted in a generation of moths all normal in wing-colour. Three pairs of these, inbred, gave rise to caterpillars which, fed like their parents on untreated leaves, developed into ninety-three moths of which seventy were normal and twenty-three melanic. From these results it seems clear that the moths' germ-cells had become so affected through the lead salt eaten by the caterpillars that the melanism could be inherited through two generations without repetition of the inducing cause, and that the factor for this condition behaves as a typical Mendelian recessive. Here we see, under the stimulus of abnormal food, the origin and transmission of a mutational character, which may be regarded as a case of partial inheritance of an "acquired change," though the sceptic may protest that it is not definitely an example of "use-inheritance," because the induced body-characters result from chemical action on the germ-plasm. The extreme abnormality of the food warns us not to attach undue importance to this interesting demonstration of germinal susceptibility. The effect is comparable to the heritable degeneration induced in some mammals after alcoholic poisoning of the parents, and must be regarded to some extent as pathological. In order to prove that use-inheritance is an important factor in evolution it is necessary to obtain inherited modifications by means of influences that are unquestionably part of the natural environment of normal living creatures.

A nearer approach to this desired result may be found in Harrison's interesting experiments on the inheritance of the egg-laying instinct in sawflies as described in his latest paper (1927). In strains of *Pontania salicis*, a common species whose larvae live in galls on willows, it was demonstrated that a certain species of plant is definitely chosen by the female fly and "that the instincts guiding the female in the choice of food-plant are germinally fixed." A race of *P. salicis* thus attached to *Salix andersoniana* was



transferred to a locality where *S. rubra* was the only willow available. The female sawflies began to lay eggs on this form, and in the course of a few years this habit became so well-established that when access to *S. andersoniana* was again made possible none of the flies showed any disposition to return to the "ancestral" plant. The "acquired habit of oviposition" on the new species had become "germinally fixed," and the sawfly race was "being forced along an evolutionary path away from the parent species."

To sum up this brief discussion on the Lamarckian factor in evolution, it must be admitted that belief in it is encouraged on account of the simple manner in which it explains—if it be a true cause—many observed facts of life. How can, for example, the winglessness of parasitic insects or the blindness of cave-insects be more simply explained than by invoking in the one case cessation of flight and in the other a uniformly dark environment? But it must be admitted that the amount of positive evidence, observational or experimental, to support belief in use-inheritance is as yet small. The prudent attitude would seem therefore to be one of open-minded scepticism, for the work of Tower, Harrison, and others has made the dogmatic scepticism which has prevailed during the past forty years about the Lamarckian factor appear unreasonable. It is certain that germinal modifications, which can be inherited, may be induced through nutritional or environmental change, but we have as yet no ground for asserting that such modifications are so strongly established in the race that they become powerful factors in the working out of evolutionary progress.

Fifty years after the publication of de Lamarck's theory, the great work of Charles Darwin (1859), to which reference has already (p. 325) been made, was published. The title of this book was noteworthy because it conveys in a few words the essence of Darwin's theory. He called it: "The Origin of Species by means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life."

Its publication was one of the most important events in the history of science, because through its influence the principle of evolution, regarded previously by most naturalists with doubt and suspicion, came to be generally accepted. Darwin's success in establishing this principle, in contrast with de Lamarck's failure, was due largely to the reasonable and convincing manner in which he marshalled the facts of structure, classification, development, and palaeontology in support of the "doctrine of descent with modification." His success was also due to the appeal made by his special theory of "natural selection" which he invoked as an explanation of the method by which evolutionary change had been brought about. Natural selection is a secondary, not a primary, factor in evolutionary change, as Darwin himself clearly perceived, for he begins his arguments by treating of variation "under domestication" and "in a state of nature," and demonstrating "that a large amount of hereditary modification is at least possible." The primary factor therefore is heredity with variation. Darwin next dwells on the importance of "the Struggle for Existence, amongst all organic beings throughout the world which inevitably follows from the high geometrical ratio of their increase." As this expression has often given rise to misunderstanding, it is important to recall that Darwin used "this term in a large and metaphorical sense, including dependence of one being on another and including (which is more important) not only the life of the individual but success in leaving progeny." From variation among living creatures and the struggle for life, thus understood, there follows the process which Darwin called Natural Selection. He points out that "of the many individuals of any species that are periodically born, but a small number can survive," and argues that the survival of some and the elimination of the rest depends on the fact that "variations . . . if they be in any degree profitable to the individuals of a species in their infinitely complex relations to other organic beings and to their physical conditions of life will tend to the preservation of such individuals and will generally be

inherited by the offspring." A creature which inherits favourable variations " will have a better chance of surviving and thus be *naturally selected*."

The theory of natural selection is not difficult to understand, and the process is certainly going on among insects as among all other living creatures. In every chapter of the present volume we have noticed examples of manifold ways in which insects are adapted in their structure and behaviour to their surroundings and to the conditions of their lives. Darwin, in his study of the problem of evolution, regarded a clear insight into the means of modification and co-adaptation to be of the greatest importance, and became " convinced that Natural Selection has been the main but not exclusive means of modification." Some of his disciples in the latter part of last century went far beyond this characteristically moderate pronouncement of their master by advocating the " all-sufficiency of natural selection." A reaction against this extreme view has gathered strength during the last twenty-five years concurrently with an advance of our knowledge of the details of inheritance and variation, so that such expressions as the " bankruptcy " of the Darwinian theory are not unknown in some quarters to-day.

Insects form a group of creatures the study of which may be especially helpful in discussions about adaptation. The rate of multiplication of many insects is so rapid that they afford striking examples of the " high geometrical ratio of increase " on which Darwin laid stress. Linné, long ago noticing the rapid reproduction of the blow-flies whose maggots feed in flesh, remarked that three of these insects could devour more quickly than a lion the carcase of a horse. Huxley calculated that, if all the progeny of a " stem-mother " aphid survived, and left offspring which all in their turn survived to propagate their kind, and so on through the successive generations of spring and summer, the descendants of that one stem-mother at the end of the season would collectively exceed in weight the whole human population of China !



The fact that aphids do not, fortunately for the human population of the world generally, increase to the extent suggested by Huxley illustrates the meaning of the struggle for existence. The food-supply of these insects, derived from the sap of plants, is enormous in extent but not unlimited, and when aphids are very numerous, the leaves and succulent shoots on which they live become dry and withered. Their piercing jaws are adapted for procuring and sucking the sap ; the wings, developed as already noted (p. 164) in many members of the virgin generations, enable them to fly to fresh feeding grounds. The green colour of many of them renders them inconspicuous to their enemies, as they feed on the leaves ; many kinds have the habit of sheltering beneath the leaves, or inducing the formation of blisters in which they obtain some degree of protection. But they fall a prey to numerous creatures of diverse kinds—insect-eating birds, ladybird-beetles and their larvae, the grubs of lacewing flies and the maggots of hover-flies, while small Hymenoptera lay eggs in the aphids' soft bodies so that parasitic larvae devour them internally. All these predaceous insects are adapted for stalking, capturing, and sucking the juices of the aphids as these are for feeding on the sap of plants, and their dependence on the aphids is shown by their increasing abundance when these are very numerous. On a single shrub hundreds or thousands of young are eliminated in every generation both among the plant-suckers and the insects of prey. We realise, therefore, that the process may be expected gradually to lead to increasing perfection of adaptation and then to ensure the maintenance of a high standard when the characters necessary to survival have been attained. It is self-evident that no characters can be attained by the race except those capable of hereditary transmission ; hence the action of natural selection depends on the preservation of favourable inherited variations through a long series of generations. The special aspect of the subject known as Sexual Selection, of importance as a factor of "success in leaving offspring," has already been discussed (pp. 201-8).

Almost any character useful to its possessors may be regarded as naturally selected in the struggle for existence ; many characters have without doubt been so selected. It must be admitted that to a very great degree natural selection helps us to understand adaptations, and in recent discussion it has been suggested that the Darwinian theory explains adaptation rather than the origin of species. The justification for this view lies in the fact that most of the characters of an insect which fit it to the conditions of its life are common to groups more comprehensive than the species—to genera, families, orders, while definitely specific characters seem often of no obvious value in the struggle for existence. Darwin pointed out the value to insects of possessing such colours, markings, and patterns as harmonise with their surroundings, and examples of “protective resemblance” have become almost hackneyed in discussions on the subject, though the keen field-naturalist can never lose his admiration at the wonder of many of them, for example, the close likeness of a large group of the Orthoptera the “stick-insects” (Plate I, A) and of the “looper” caterpillars of Geometrid moths (Plate X, A) to twigs the colours of many of the latter simulating the lichens that encrust the bark. We have previously mentioned (p. 273) the resemblance of the upper forewing surface of many moths to dead leaves, tree-bark, and similar objects on which the insects rest. Such resemblance is the more striking in cases where the hindwings are brightly coloured as in the “yellow underwing” and “crimson underwing” moths, the brilliant areas of the wings being entirely hidden when the moths are at rest. These protective colours and patterns are in the main common to groups of species ; for a conspicuous discriminative character between two species we must often depend on some feature of no value at all as an adaptation to environment. Of our two large, common British yellow underwing moths, for example, *Triphaena pronuba* is recognised by the narrow and *T. orbona* by the broad, dark border to the flaring orange-yellow of the hindwings. Turning to larval stages

of Lepidoptera, we find the large caterpillars of the hawk-moths (Sphingidae) of a predominantly green (sometimes brown) shade, the area broken by series of oblique, dark, lateral lines—the whole aspect definitely protective among leaves or on twigs. Our two common species of *Smerinthus*, *S. populi* and *S. ocellatus*, have green caterpillars closely alike in size, colour, markings, but while the horn on the eighth abdominal segment of the *populi* larva is green like the body generally, that of the *ocellatus* larva is blue. It is impossible to regard such differences of any importance in the struggle for existence, and if specific distinctions be due to the action of natural selection they must be not merely important but so important as to decide the alternative of survival or destruction. The only suggestion that has been made to connect characters of this kind with natural selection is the possibility that they may be correlated with characters that possess “survival value” so that the one cannot be inherited without the other. This possibility cannot be dogmatically denied, but can such correlation be reasonably regarded as likely? Among insects of very different type from the Lepidoptera—the wingless shore-haunting Collembola or springtails—similar facts can be observed. The same mass of wrack at high drift-mark often harbours hundreds of two species of Achorutes, *A. viaticus* (Fig. 66) and *A. longispinus*, distinguished by constant structural features in the feet and spring and by the much longer anal spines of the latter (Fig. 81), yet living amidst identical surroundings to which either kind seems as well suited as the other.

Yet there are doubtless many cases in which careful study of an insect's habits tend to prove that characters not obviously useful may be really of value in the struggle for existence. Taking for example the African nymphalid butterflies of the genus *Precis*, a number of forms once regarded as distinct species were shown by G. A. K. Marshall (1896, 1898, 1902) to be alternating seasonal phases of the same markedly variable insect. *Precis octavia*, a butterfly with wings predominantly salmon-pink, black



bordered, and spotted above and below, is the wet-season form of the insect known in the dry season as *P. sesamus*, which has the wings above dark blue with many black markings and sub-terminal rows of red spots, while below they are uniformly dark and mottled so as to resemble dead leaves; this likeness is intensified by the markedly falcate tips of the forewings, these being evenly rounded in *octavia*. Hale Carpenter (1920), in his recent work on African insects, confirms the opinion of Marshall and Poulton that the dry-season forms are the more definitely protectively coloured ("procrptic"), "and that this is due to the operation of the dry season, when insects are so scarce that insectivorous animals need to work harder to obtain food, and the risk to any particular insect is proportionally greater." Though the two forms *Precis octavia* and *P. sesamus* (Plate XIV, A) are only seasonal varieties, the difference between them is much more conspicuous than that which exists between thousands of undoubtedly distinct species nearly allied to each other.

Protective resemblance in general may therefore be confidently regarded as adaptive, whether or not the distinctive features causing the resemblance are of specific importance. There is another set of facts connected with the coloration of insects to which H. Bates (1862) was the first to call attention. Certain groups like the wasps among the Hymenoptera, and several sub-families of Nymphalid butterflies—Danainae, Ithomiinae, Acraeinae, and Heliconiinae—are arrayed in a livery of startlingly contrasted colours and are thus rendered very conspicuous. Such appearance is now generally defined as warning ("aposematic") colour or pattern, and is frequently associated with the possession of noxious qualities of some kind; wasps have stings and many of the butterflies of the groups just mentioned produce poisonous or repellent secretions which render them distasteful to lizards, birds, monkeys, and other creatures that eat butterflies. The warning colour is believed to be advantageous to such insects, because it ensures that they are rapidly recognised by possible enemies and left alone. Bates noticed that certain Brazilian butterflies, belonging to

families or sub-families quite distinct from the noxious insects, resemble them so closely in general aspect that they may be regarded as "mimics," and by means of the mimicry it is believed that their aspect deceives insect-eating creatures which accordingly leave them alone, although they are innocuous and edible. It is also well known that noxious insects of one group may be "mimics" of members of another; many species of tropical American *Heliconiinae* are closely like species of *Ithomiinae* inhabiting the same districts. This type of mimicry was first distinguished by F. Müller (1879), who explained the advantage derivable from these resemblances between protected forms as being "the division between two species of the percentage of victims to the inexperience of young insectivorous enemies, which every separate species, however well protected by distastefulness, must pay" (R. Trimen, 1897). A "mimicking" species less abundant than its model will only pay toll in proportion to its numbers in any area, as compared with the heavier mortality suffered by the commoner species from the attacks of insectivorous creatures. Another remarkable fact about mimicry among butterflies is that it may be restricted to the female sex; this is well illustrated by nymphalines of the genus *Hypolimnas* in the eastern tropics, whose males are of the aspect typical of their group, while the females mimic various *Danainae*, and also by the African *Papilio dardanus*, which, besides a typical form of female resembling the male in her cream and black "tailed" wings, possesses various "untailed" female forms each a close mimic of some *Danaine* or *Acraeinae* butterfly inhabiting the same district.

Mimicry among insects, and especially among butterflies, has been prominent during recent years in discussions between naturalists of the Darwinian school who uphold the theory of natural selection and others, like R. C. Punnett (1915), who contend that mimicry has no adaptive meaning and that it can be explained by the influence of the surroundings or by the inheritance of mutations on Mendelian principles. That inheritance among the poly-

morphic species like *P. dardanus* does follow Mendelian laws is established, but this does not oblige us to deny the adaptive value of mimicry, which has received strong support from the recent field investigations of G. A. K. Marshall (1902, 1909), C. F. M. Swynnerton (1919), and Hale Carpenter (1920, 1921).

The value of mimicry to butterflies that display it depends clearly on the danger which they might incur from birds and other creatures, and opponents of the selection theory have often denied that these insects are commonly pursued by predaceous enemies. Mimicry can have no protective value unless insects "warningly" coloured are for the most part left alone by creatures that freely catch and eat insects not so advertised as noxious. Ever since Bates' observations became well known this generalisation has been affirmed by some and denied by others who have had opportunity of observation; the long-continued, systematic investigation necessary for deciding the point has only been undertaken in recent years. Experiments in offering various butterflies to birds are largely affected in result by the bird's condition, whether of hunger or repletion, and general statements by observers that they have never seen a bird eat or pursue a butterfly do not in themselves afford negative evidence of any value. As Hale Carpenter remarks, "attacks on butterflies may very easily be overlooked unless an observer is especially on the look out for them." Marshall has collected a number of records on this subject and made careful personal observations in England and in tropical Africa. As might be expected, swallows and flycatchers seize and devour butterflies constantly. An especially interesting British observation is that the Kestrel swoops on butterflies resting on the ground and seizes them; in the south of England this small hawk has been watched in the act of taking large numbers of a "fritillary" (*Argynnis aglaia*) and the "Marbled White" (*Melanargia galatea*). Hale Carpenter records how he watched wagtails in tropical Africa feeding on butterflies; a single bird devoured eleven in three minutes, and



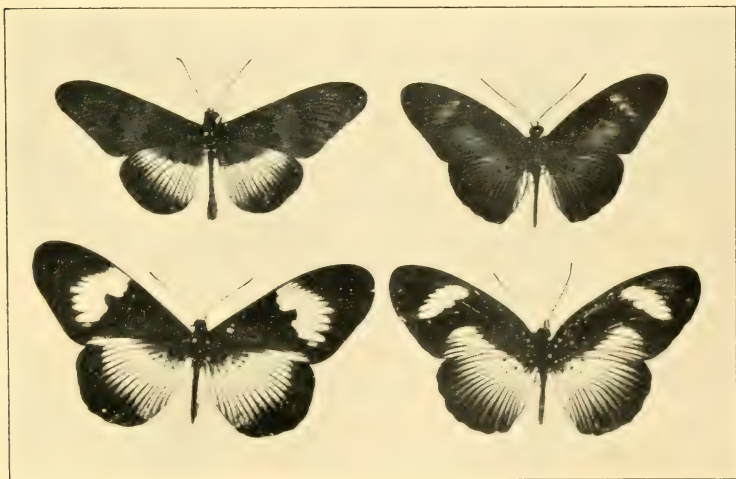
Pieridae and Lycaenidae were definitely selected for capture "from among a crowd of butterflies settled on the mud," the noxious and mimetic insects present being left alone. He also draws attention to the severed wings and fragments of butterflies left by birds after hunting and eating them, and the neat triangular nick often seen on both hindwings of some butterfly that escaped from a pursuing bird at the cost of those fractions of its wings caught by the bird's beak. That choice is commonly exercised by insect-eating birds is shown by Swynnerton's observations. He admits that absolute inedibility among butterflies is very rare, and that a hungry bird will seize a specimen of the large, conspicuous black and white-winged African danaine *Amauris niavius* in preference to the nymphaline *Precis cebrene*; but he insists that birds as a rule "only eat *Amauris* when hungry, but *P. cebrene* nearly to repletion-point." The advantage of such comparative inedibility must be great, "sufficient to make the possessor worth mimicking," as "shown by the immense meals that are sometimes eaten after the refusal of a low-grade butterfly; e.g. forty butterflies, including fourteen large *Charaxes*, by a roller after she had neglected a *Mylothris*, and thirty-seven, including twelve large *Charaxes*, after rejection of a *Terias*." Hale Carpenter (1921) records the result of systematic trials with two monkeys, offered a large selection of insects of various orders, some with the concealing and others with the conspicuous type of coloration. The two monkeys were offered altogether 375 insects, of which 155 were ascribed to the former and 220 to the latter type. Of the 155 procryptic insects 113 were eaten and 42 refused, while of the 220 conspicuous insects only 44 were eaten, 176 being refused; so that the reaction of the monkeys with regard to the two types of insect agreed with expectation in 73 per cent. of the specimens in the one group and in 80 per cent. of those in the other.

Of the many cases of mimicry now well known to students of insects, that of *Pseudacraea* and *Planema*, elucidated in recent years by K. Jordan (1910), H. Eltringham (1910), and Hale Carpenter (1920), has the most

# PLATE XIV



A. WET AND DRY SEASONAL FORMS: *Precis octavia* (left) and *P. sesamus* (right). Upper and lower surfaces, S. Africa. Three-fifths size.



B. *Planema macarista*, "model" (left), and *Pseudacraea eurytus*, "mimic" (right), West Africa. Males above, females below. Half size.

To face p. 374.]

[H. Britten, photo.]





definite bearing on the problem of selection. *Planema* is a genus of Acraeine butterflies with a wide range over tropical Africa, comprising a number of species whose wing patterns are predominantly black and white in the female, black and tawny with red markings in the male. *Pseudacraea* is a nymphaline genus closely akin to our south English *Limenitis sibylla* ("White Admiral"), it appears through Africa in a number of forms, the males and females closely mimicking the various *Planema* "models," not only in wing-pattern but in the constant sexual difference of narrower forewings in the male than in the female (Plate XIV, B).

The various mimetic forms of *Pseudacraea* received distinctive names and were all regarded as distinct species, until Jordan's studies of the variations convinced him that most of them were referable to the Linnean *Pseudacraea eurytus*. This view has been confirmed by Hale Carpenter's success in breeding and rearing various forms from the same parents. He has also demonstrated the selection-value of mimicry by statistical records, taken on the shores and islands of the Victoria Nyanza, of the numbers of the *Planema* models and of the *Pseudacraea* mimics as compared with intermediate forms which show no close resemblance to any *Planema*. In localities and seasons when the proportion of *Planema* to the total number of butterflies captured is high, the proportion of the intermediates to the total number of *Pseudacraea* is low; but when the *Planema* models are relatively few, the number of intermediate *Pseudacraea* becomes relatively high. From these figures it is inferred that the intermediates "were apparently destroyed while the models exercised their protection to the mimetic forms," but that they had "an equal chance of survival . . . when the protection of the models was in abeyance."

From the facts of insect life summarised in the preceding pages, and from many others that could be adduced, it seems certain that natural selection has played a large part in the evolution of insect races, and in the fixation of specific characters so far as these are themselves adaptive, or

correlated with characters that are adaptive. Among creatures such as insects in which reproduction is very rapid and the number of individuals is often enormous, natural selection must be an especially potent agency. For the many characters as to whose utility there is no evidence, we may find some explanation in the facts of mutation and Mendelian inheritance. Unfortunately a tendency has shown itself during recent years for investigators of the different possible factors of evolution to minimise or deny the importance of those factors in which they are not themselves actively interested. "Darwinism" and "Mendelism" (the terminology is suggestive of partisan or sectarian controversy) are in fact complementary rather than rival theories of evolution, for the former helps us to understand, in part, adaptive and the latter non-adaptive characters. Much discussion has taken place as to whether large or slight variations are to be considered the more important as "raw-material" for the action of natural selection, and many advocates of the Darwinian theory seek to emphasise the importance of slight, "almost imperceptible" distinctions; this was the later view of Darwin himself, although at one time he thought that what would now be called mutations might be of great value in evolution. A variation whether extensive or slight will, if favourable, be selected for survival, and if heritable be transmitted to future generations. It has already been pointed out (p. 355) that definite segregation in inheritance rather than extent is to be taken as the mark of a discontinuous variation or mutation, and Hale Carpenter has shown (1914) that small variations in wing-pattern of the mimetic butterfly *Papilio dardanus* are definitely inherited.

The limits of all classificatory groups—species, genera, families, and the rest—vary greatly in clearness of definition; where the distinctions are most clearly marked it is likely that many intermediate forms have died out. Yet we have seen that such a striking character as winglessness commonly shows itself in a single generation. It is interesting to find that sometimes a character that may be regarded as generic

appears in a variety of some common species. We may take an example from the springtails of the genus *Achorutes* mentioned in a previous chapter (pp. 264–6). The species of *Achorutes* have, as a common character, a pair of spines (Fig. 81, *a*) at the tail end of the body, longer in some species, shorter in others. Other genera of the same family have no spines, or three, or four, as a distinguishing feature. Yet in several species of *Achorutes* a few examples out of a large number may have no spines at all, or there may be a third median spine (Fig. 81, *b*) developed between those of the normal pair. Such facts are suggestive of the possibility of rather quick change in the history of a race; but it must be remembered that for a new genus to arise in this way,



FIG. 81.—Tail-end of Springtail (*Achorutes longispinus*) Spitsbergen. *a*, normal two-spined specimen; *b*, three-spined variety.  $\times 300$ .

further distinctive characters would be necessary and the creatures possessing them would need to “breed true.”

In the course of the early controversies that raged during the last century around the evolution problem, it was often urged by opponents of Darwin that incipient species could never be established, as they would be “swamped by intercrossing.” The segregation brought about through Mendelian inheritance disposes of this objection, and in the case of various insects—*Amphidasys* and *Drosophila*, for example—already used in illustration, we see how the new form is preserved in a pure strain. Such a result may be regarded as a kind of germinal isolation; the importance of various types of isolation in the fixation of systematic differences was emphasised by G. J. Romanes (1897), and as



a result of the study of regional variation among insects, as among other groups of animals, increased attention is being given to this factor. The famous "Large Copper" Butterfly (*Chrysophanus dispar*) of the East Anglian fens, extinct for the last sixty years, is apparently unknown on the Continent, and opinion is divided as to whether it should be regarded as an "insular sub-species" of the central European *C. rutilus* or a distinct but closely allied species. The large Chinese Saturniid silk-moth *Philosamia cynthia* is represented in Japan and Java by readily distinguishable forms (*P. pryeri* and *P. insularis* respectively), which are also regarded as "good" species by some students and as sub-species by others. *Actias selene*, an Indian moth of the same family, with wings of a predominantly pale greenish-cream colour, has a sub-species *A. calandra* on the Andaman Islands with bright yellow wings in the male. Such changes in isolated "colonies" of certain insects may be explained as due either to strongly impressed environmental influence or to the probability that the germinal constitution of the small isolated group differs from that of the main continental stock. Besides geographical isolation, seasonal change in the breeding season serves to segregate incipient species, and so do modifications in the pairing organs of a variety developing from a parent race; this last-named feature is well illustrated by the two forms of British wasps, *Vespa rufa* and *V. austriaca*, described in a previous chapter (pp. 234-6). Such modifications tend to result ultimately in mutual infertility and complete prevention of pairing, as K. Jordan (1896) pointed out in his exposition of "mechanical selection."

Insects far outnumber both in kinds and individuals all other known animals now living on the earth and in the waters taken together. Their individual lives are relatively short and the numbers of their successive generations in the course of the world's history must therefore have been enormous. Since the far-off Devonian Period at least, the evolution of the class has been going on, and long before then the most primitive insects must have diverged from the

early Arthropodan stock. As to the course and method of the long life-story of insect races we still have much to learn ; it is cheering to realise that in the facts of structure and function, reproduction and inheritance, modification and adaptation displayed in the insects around us to-day we have some clues to help us in the solution of great and fascinating problems.

## CHAPTER XIII

### INSECTS AND OTHER ORGANISMS

THE subjects considered in most of the chapters of this book—feeding, shelter, reaction, and relation to surroundings, family and social life, and especially the implications of the struggle for existence discussed in the pages immediately preceding—have combined to emphasise the importance of other organisms, both plant and animal, in the life of insects and also the importance of insects in their lives. A vast number of insects feed, for example, on plants, with the result that many herbs, shrubs, and even trees are destroyed by them. Some plants have acquired the power of response to the insect's presence and stimulation in the formation of a special growth or gall, thus providing the insect with food and shelter at the least possible disadvantage to the plant. Such insects as bees and Lepidoptera which have developed specialised modes of feeding on floral products, often benefit the plants that they frequent by pollinating the blossoms and ensuring the setting of seed. The plant-eating insects are pursued and devoured by predaceous insects or invaded and destroyed internally by parasitic members of their own class, or eaten by relatively big creatures such as birds. Many insects again live as parasites in or on the bodies of larger animals, and themselves harbour minute parasitic worms and protozoa. In this chapter it is proposed to discuss only a relatively few examples of definite relations between insects and other creatures that have an evident bearing on the conditions of their lives.

The interrelations between the various organisms inhabiting any region become increasingly complex when



the number of individuals and kinds is very great, as they are in an English woodland during summer and still more in a tropical forest. A clearer view of what happens is afforded by the intensive study of a less thickly populated region, and a full account of the mutual life-relations of a group of arctic creatures including a fair number of insects, is now available in V. S. Summerhayes and C. S. Elton's work (1923) on the ecology of Spitsbergen. We have referred more than once to some of the springtails of that archipelago ; now it will be profitable to see their part and that of other insects in the general life-drama of the district which they inhabit. The scattered plants growing on the stony slopes of these northern islands afford shelter to various springtails and the larvae of small Diptera ; these insects eat the vegetable tissue either in the fresh or decaying state. The mosses and other lowly plants of the bogs and wet tundra supply food for another association of Collembola and grubs of flies ; and so do the lines of *Fucus* at and above the tide-marks, as previously mentioned (p. 283). Dwarf-willow serves as feeding-ground for a few sawfly caterpillars, and some parasitic Hymenoptera lay their eggs in the various plant-feeding larvae. On the leaves and blossoms of the Mountain Avens (*Dryas octopetala*) a single species of Aphid (*Scaeva dryadis*) lives by sucking sap, and a hover-fly (*Syrphus tarsatus*) haunts the neighbourhood, for its maggots feed on the aphids. Erratic ice-borne boulders are of interest in that they " possess self-supporting communities of their own." On them grows a flora of mosses, lichens, and algae among which live small, pale springtails (*Folsomia iv.-oculata*). These eat the vegetation and are in their turn devoured by two small spiders and two predaceous mites. Many of the insects, as well as the spiders that feed on them, may fall victims to such birds as Sandpipers and Snow Buntings, which themselves serve as prey to the Arctic Fox ; the latter animal is not infrequently hunted and eaten by the Polar Bear, and thus the small insects of these arctic lands form links in the food-chain or " nitrogen-cycle " which passes from the sparse vegetation to one of

the largest of beasts of prey. The birds and mammals may, of course, be infected with Mallophaga, Anoplura, and other insect parasites, but there is another possible life-connection between birds and small insects. Glaucous Gulls use moss largely in their nest-building, and two or three species of springtails are to be found in the nests, as well as specimens of a midge (*Leria septentrionalis*) and its pupa, found also in similar connection in St. Kilda; it is suggested that there is definite benefit to the midges in this association as "the warmth of the sitting birds would speed up the flies' development." The presence of large bird-communities is indirectly favourable to an increase in the numbers of many insects, because the droppings of the birds lead to luxuriant growth of the plants in which the insects find shelter and food.

The importance of birds' nests as shelter for insects is well illustrated by the observations of R. L. Praeger and others (1915) on the natural history of The Bills, a group of rocks off the Atlantic coast of western Ireland, situated 9 miles N.W. of Clare Island opposite the entrance to Clew Bay and 8 miles S.S.E. of Achill. These islets attaining a height of about 120 feet above sea-level are largely wave-washed as well as wind-swept. In addition to the Common Earwig, probably blown over in flight, their observed insect fauna consisted of a single ant, seven beetles, a bristle-tail, and three springtails, most of which were found in the nests of Puffins and Gulls. It is likely that their presence on these remote rocks is largely due to accidental carriage on the feet of birds across "the intervening sea," and affords an example of the manner in which insects are helped by the flight of birds to extend their range.

Insects, like animals generally, depend either directly or indirectly on plants for their food-supply. Few plants are utilised by insects to a greater extent than oak-trees are; it has been computed that over 500 kinds of insects feed on oak in various ways. The leaves are eaten by caterpillars of many Lepidoptera, the most notable of which, in our own country at least, is the small Green Bell-Moth (*Tortrix*

*viridana*). These moths are flying at midsummer, and after pairing lay on the twigs their eggs which are not hatched until the succeeding spring. In May and early June the small slaty caterpillars feed in thousands on the leaves, and in many seasons the trees are completely stripped of foliage. The caterpillars make for themselves cylindrical shelters, each rolling round the tip of a leaf and fastening it by silken threads; in this little case the caterpillar has a house, the walls of which are good to eat. A shock to the leaf may result in the caterpillar crawling out of its shelter and lowering itself to the ground, playing a thread of silk out of its mouth; by means of this thread the larva can climb up again when conditions once more become normal. The leaf-shelters serve also to protect the pupae. An oak-wood where these caterpillars have been present in multitudes—as they often are in hot seasons—looks, with the brown and withered remnants of its leafage in early summer, as if scorched by fire. It has been pointed out by A. T. Gillanders (1912) and others that it is the pedunculate form of our native oak which suffers especially from the ravages of these insects, the sessile variety being comparatively immune, perhaps because coming earlier into leaf it can better afford to pay toll to the caterpillars. Such conditions vary in different areas, and it appears generally that trees suffer most severely when their sprouting season coincides with that of the hatching of the insect larvae which devour them. The larvae of *Tortrix viridana*, though usually restricted to oak, can feed on the leaves of other trees; ash, beech, lime, and hazel, for example. They have been observed to forsake oaks whose leaves they had completely devoured before they had attained full growth, and to migrate to some other trees. The foliage of oaks is also eaten by caterpillars which can live and flourish on a variety of deciduous trees; the Buff-tip (*Pygaera bucephala*) and the Vapourer (*Orgyia antiqua*), for example. There is obvious advantage for an insect that is adaptable in its feeding habits and not absolutely dependent on one plant only for its sustenance. The “Vapourer” has some



interesting adaptations to the conditions of the woodland trees on which it feeds. The moths, which have reduced mouth-parts so that they cannot feed, are seen in autumn ; the males brown-winged with white spots flit around the trees on the twigs of which rest the fat wingless females clinging to the silken cocoon surrounding the now empty pupal coat. After pairing the female lays on the cocoon her mass of eggs which are the wintering stage for this species. The " tussock " caterpillars, hairy, bristly, and conspicuously coloured, are hatched in spring. They are active and well protected so that they can set forth on migratory journeys, passing on occasion from tree to tree or crossing roads or clearings in their search for fresh feeding-grounds, their activity compensating for their mother's inability to extend the range of the species.

The timber of oak and other forest trees is tunnelled and eaten by the larvae of many long-horn beetles and bark-borers, as well as by the caterpillars of various moths. Of the latter the large black-headed, pink and yellow caterpillar of the Goat Moth (*Cossus*) is the most formidable, attaining a length of three inches or more, taking three or four years to complete its growth, and feeding voraciously in the trunks and branches. The strong jaws of these caterpillars enable them to " tunnel right into the heart of the hardest wood," and as two hundred of them may occur in a single trunk their activity can end only in the death of the tree which harbours them. This result raises the question of the relation between the growth and multiplication of the insect species and their food-supply. In extensive forests where the mass of foliage and timber furnished by the trees seems inexhaustible there is no practical limit to the increase in number of an insect which has freedom to migrate in some stage of its life-history. Where migration, however, is restricted or impossible, excessive multiplication of an insect may lead to the complete or partial starvation of some individuals. This condition is shown in the dwarfed specimens of some of our common tree-feeding geometrid moths, *Hybernia defoliaria* for example, developed in certain

years from caterpillars which have been obliged to "feed up" and pupate on an inadequate supply of foliage late in the season.

Oak-trees are of special interest in a discussion on the relations between insects and plants, because they have, to a greater extent than any other tree or shrub, become adapted to the presence of certain insects, so that by the formation of galls they provide these insects with food at the least possible expense and disadvantage to their own health and well-being. A gall is an abnormal plant-growth, incited by the influence of an insect on the plant's formative tissue, which develops under the chemical or tactile stimulation in such a way that the insect is provided with shelter and food without the necessity of destroying large quantities of foliage or wood. Most by far of the galls on an oak are due to the small Hymenoptera of the family Cynipidae, generally known as gall-flies. Every one knows the sub-spherical "oak-apples," the smooth, woody "marble galls," the succulent "cherry-galls," and the round, flattened "spangle-galls," on or under the leaves, while many-chambered hard galls are to be found on the roots. These are only a few of the multiplicity of growths on oak due to various Cynipidae. Though galls are abnormal from the purely botanical point of view, each has a definite specific form, so that the particular causative insect can be determined from the result of its action on the plant. It was formerly thought that the stimulation leading to gall-growth must be due to the puncture of the plant tissues by the female fly's ovipositor, or to some irritant fluid injected when the egg is laid. But the inciting cause for cynipid galls is now determined as the feeding and digestive functions of the larva. There will be no growth of a gall if the egg be removed; growth begins after the hatching of the larva and then larva and gall grow together. A. Cosens (1912) has elucidated the physiological processes accompanying gall-formation. The egg is often laid in or near the plant's formative tissue (cambium), and on this the grub when hatched begins to feed, sucking out the cell-contents, so

that the cells close to the larva collapse, leaving a cavity which becomes the chamber of the gall. The grub's salivary secretion, largely poured out on the cambium, hastens the change of the starch of the plant-cells into sugar ; thus the formative cells are incited to rapid multiplication and the resultant growth of the tissue leads to the formation of a gall. Direct action on the cambium does not, however, always occur ; "any actively growing tissue will respond" to the gall insect's presence and the stimulation may work "on tissue at a considerable distance from the centre of application." It remains doubtful why each gall should have its specific form and texture, though mechanical considerations may afford some clue to the problem. Cosens suggests as a factor the direction in which stimulation is applied so that a gall of spherical form may be expected as the result of influence "about equally distributed in all directions."

An especially remarkable feature in gall-formation is presented by the differences in position, shape, and texture observable in galls produced at different seasons by alternating generations of the same species of gall-fly. These seasonal forms of insects of the same kind differ markedly from one another, so that there has been established a wonderful reciprocal rhythm of growth and change between the insects and the trees. The alternating seasonal generations of many common British gall-flies are described by H. Adler and C. R. Straton (1894). The grubs which are found in early summer within the "oak-apple" (Plate XV, A) develop after pupation into a gall-fly known as *Teras terminalis* with winged males and wingless females. After pairing the females go underground and lay their eggs in the oak-roots, whereon, after the hatching of the larvae large root-galls (Plate XV, B), are formed in which the grubs live and grow through the winter, being finally transformed into adults, which being all females and all wingless, were formerly regarded as belonging to a genus and species distinct from those of the oak-apple gall-flies and known as *Biorhiza aptera*. It has now been shown that these virgin



PLATE XV



A. OAK "APPLES" GALLS OF *Teras terminalis*.



B. ROOT-GALLS OF ALTERNATING GENERATION (*Bierhiza aptera*).  
Half size.

To face p. 386.]

J. W. Nixon, photo.



wingless females lay their eggs in the buds of the oak-trees ; the result is, that after the grubs are hatched, oak-apples form on the developing shoots, whence, as already mentioned, male and female Teras-flies emerge next summer. Thus the two quite dissimilar sets of insects, one sexual and the other virgin, are alternating forms of the same species, each generation beautifully adapted to the seasonal cycle of the tree on which it lives. A similar alternation is shown in the life-history of the cynipid which produces the large yellow or reddish "cherry-galls," conspicuous on oak-leaves from July onwards, becoming brown and "ripe" in October. From the larvae feeding within these are developed, for emergence in midsummer, virgin female gall-flies (*Dryophanta scutellaris*), which pierce the resting buds and lay their eggs within. As a result of the larval stimulation, the affected buds, instead of developing into shoots, become enlarged and swollen and violet in colour. The larvae feeding within develop by spring or early summer into the sexual brood of flies called *Spathogaster taschenbergi*, the females of which pierce the leaf-tissue of the oak with their ovipositors, the presence of the grubs, when hatched from their eggs, leading to the formation and growth of the cherry galls in late summer and autumn.

Galls made through the stimulation of cynipid grubs are often inhabited by larvae of other insects. Several genera of Cynipidae (*Synergus* for instance) have the habits of inquilines or "cuckoo-parasites," laying their eggs in galls already formed so that the larvae may feed within ; in many cases there is sufficient provender for both "host" and "guest." Cosens has found that some of these inquilines "possess the gall-producing power" in a reduced degree. C. R. Osten-Sacken long ago (1863) drew attention to the close resemblance frequently observable between a true gall-fly and its inquiline. "The one is the very counterpart of the other, hardly showing any difference except the strictly generic characters." Then there are the true parasites—a few belonging to the Cynipidae, but most to the Chalcididae and other families of Hymenoptera—



whose females lay their eggs in the galls, so that the grubs may devour the inhabitants whether hosts or inquilines.

Gall-formation on plants is brought about as a response to the presence of many other insects besides Cynipidae. The sawflies (Tenthredinidae), also belonging to the Hymenoptera, have a number of gall-dwelling species; the succulent fruit-like growths often seen beneath the leaves of willows harbour caterpillars of *Pontania*, a genus of the Nematine section of the family. Here the abnormal plant-growth seems to result from the egg-laying. The gall-midges (Cecidomyiidae), a family of small Diptera, comprise hundreds of species whose larvae live in characteristic galls formed on various kinds of plants. On willows, for example, the little pinkish grubs of *Rhabdophaga heterobia* may be found crowded among the small rosette-like hairy leaves of the arrested shoots, while the larvae of the allied *R. saliciperda* feed in small oval chambers in the outer layers of the wood; when transformation is completed their empty white pupal cuticles project from the surface of the bark. In female gall-midges the hinder "telescoped" segments of the abdomen are very elongate, so that the slender tip can be inserted between young leaves or elsewhere that may be suitable for egg-laying. The Pear-Midge (*Contarinia pyrivora*), for example, pushes her long, tapering tail-region into a blossom-bud in early spring and the grubs hatched from her eggs feed in the young fruitlet. In this case there is no true gall-formation; the little infested pears become shrivelled and stunted, and usually fall to the ground early in the season. The full-grown pear-midge grubs have the habit of bending their bodies sharply and then suddenly straightening them; thus they are enabled to leap out of the pear, whether it be fallen to the ground or still on the tree, and to reach the surface of the soil into which they burrow for pupation. Here, again, the form and behaviour of the insect, both in the larval and winged stages, ensures its adaptation to the plant on which it is dependent.

An interesting development in the relations between

insects and the plants on which they feed is to be noticed where a species of insect passes from one kind of plant to another and back again in the course of the yearly life-cycle. Many aphids or greenfly afford well-known examples of such complex adaptation. In previous chapters (pp. 138-9) we have noted the general yearly course of the generations of these insects; the autumn sexual forms, the hard-shelled winter eggs, the early spring stem-mothers, and the successive generations of virgin females giving birth to active young through the spring and summer months—the latest of these being the “sexuaparae” or parents of the autumnal sexual brood. It will be remembered that the early virgin families in the spring consist largely of wingless insects, but that soon a number of winged aphids are developed which fly away to other plants, and in this way extend the feeding range of the species. While the winged members of some aphid races fly only to plants of the same kind as that on which they were born, others seek plants of quite a different kind whereon the successive virgin broods of the summer feed and grow and multiply. These latter are known as migratory aphids, and it may reasonably be believed that the migratory habit, by putting two distinct kinds of plant under contribution at different seasons of the year, is definitely beneficial to the insects. The common green aphid of the apple (*Aphis pomi*) has been generally regarded as a non-migratory species; all the virgin generations, as well as the sexual forms, may be found living and feeding on orchard trees. E. M. Patch, however, has lately demonstrated (1923) that in the northern United States, large numbers of this species occur on a wide variety of plants—Polygonum, Crucifers, Clovers, Mallow and Carrot, for example, as well as on rosaceous trees. Another apple-feeding aphid (*Siphocoryne avenae*) is migratory. Its autumn sexual brood, winter eggs, stem-mothers, and one or two early virgin generations live on the apple-tree, but the winged spring migrants fly away to cornfields and spend most of the warm season of the year feeding on oats, often penetrating into their flowers.

Later, aphids are born which develop into winged autumn migrants ; these fly back to the apple-trees, where the sexual forms are born and, when mature, pair in preparation for the winter eggs.

The bark-lice (*Chermesidae*), a family of Hemiptera closely allied to the *Aphidae*, afford interesting examples of insects with a complex life-cycle adapted to two distinct types of coniferous trees, with the formation in certain generations of remarkable galls. *Chermes* differ from Aphids in its mode of reproduction, as egg-laying is practised by all the virgin generations as well as by the mated females. In most species of *Chermes* whose life-cycles have been investigated, by A. Cholodkowsky (1907), C. Börner (1908), H. M. Steven (1917), and others, the sexual forms are developed on the Spruce, which is consequently known as the "principal host" plant of the insects. Both sexes are wingless, and after pairing each female lays a single egg which hatches in late summer ; the first-stage young winter on the buds of the tree, their long piercing stylets inserted into the tissues. In the succeeding spring they begin to feed vigorously, and in less than a month become mature "foundresses," all this generation being virgin females, each of which lays a number of eggs and then dies. The tree responds to the stimulus of their sucking action and salivary secretion by forming a chambered gall like a small cone or pine-apple within which the young develop from the eggs which the foundresses laid. As these young grow and develop within the gall chambers during summer they are known as gall-dwellers ("*gallicolae*"), but before the last moult they come out on to the leaves and ultimately acquiring wings fly away from their native spruce to some other coniferous tree—larch, pine, or fir—as "migrants." They are all females and lay their eggs on the larch or other "intermediate host" tree ; the young in their first stage hibernate, with their piercers thrust into the bark or leaves, and become mature in spring as "colonists"—wingless, virgin females which in their turn lay eggs ; from these are hatched young which may develop quickly by midsummer



into the winged "sexuaparae" that fly back to the spruce and there lay the eggs, whence the wingless sexual forms are hatched and matured by August. Thus the life-cycle from one sexual generation to the next lasts for two years. A most interesting feature of the *Chermes* development, however, is a tendency to omit from the normal series of generations, several of the broods. Thus there are races or species of *Chermes* in which the winged offspring of the foundresses remain on their native tree or fly to other spruces, and from their eggs are developed foundresses like their parents; in such cases there is a succession of two alternating virgin female generations on the "principal host" tree, the migratory habit being, at least for a time, abandoned. On the other hand, the offspring of colonists on the larch or pine may develop, not into winged sexuaparae destined to fly back to spruce, but into wingless "exiles" which remain on the "intermediate host" tree. There may be several generations of exiles on larch or pine through the summer, and in the autumn are hatched young which after wintering without a moult, develop next spring into a new brood of colonists. Here, therefore, the series of generations is restricted to the virgin forms characteristic of the larch or pine. It is of great interest to see such a tendency towards the simplification of a life-cycle normally very complex; again we are convinced of the plasticity possible in the behaviour of insects so that their relations with the plants whereon they live may become modified in various ways; and as the successive broods of *Chermes* are differentiated by special structural features we realise that the dropping out of several generations from the normal cycle must be accompanied by some determining germinal change. This may conceivably be brought about as a response to the changing conditions of the insect's food-plant seasonal or otherwise. A. D. Imms (1925) suggests that the main factor determining the migration of aphids "appears to be those physiological changes in the plant during growth which render it unsuitable as a host," and that "temperature may possibly exercise an influence on the behaviour

of the chromosomes." We have noted in a previous chapter (p. 139) that the production of sexual or virgin forms

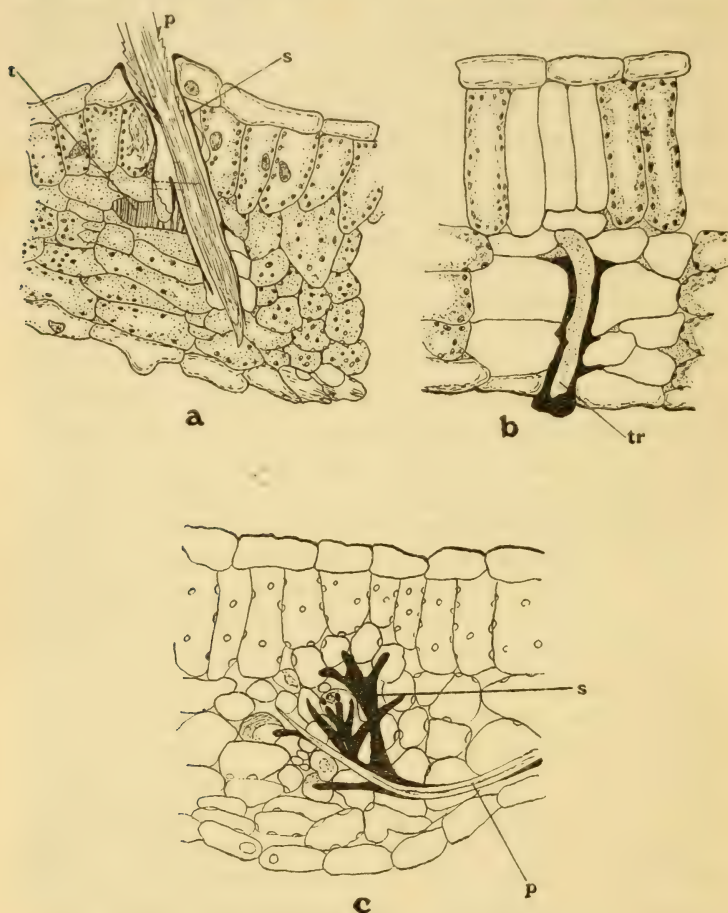


FIG. 82.—Sections through Potato-leaves pierced by Hemiptera. *a*, piercing stylets (*p*) of Leaf-hopper (*Eupteryx*) penetrating tissues, *s*, sheath of hardened saliva, *t*, tracheid; *b*, puncture by *Eupteryx* at lower surface, saliva surrounding track (*tr*) of piercers; *c*, piercers of Mealy-bug (*Dactylopius*) with branching tracks in phloem shown by saliva.  $\times 600$ . After K. M. Smith (*Ann. Appl. Biol.* xiii, 1926).

follows from alternative modes of nuclear behaviour, and it is possible that the germinal modifications for such changes

in these insects may be responses to the environmental stimulation from food or temperature.

Reference has already been made to the destructive effects on plants due to the feeding of insects. Such effects are obvious to all observers in the ravages of leaf-eating caterpillars or wood-boring beetles. Sucking insects such as the aphids, plant-bugs, and their allies, pierce the plant tissues to obtain sap, and the result of their feeding habits may often be seen in withered, rolled, or blistered leaves. Recently some attention has been given to the details of the action of sucking insects on plants, and reference may be made to the researches of J. Davidson (1923) and K. M. Smith (1920, 1926). It appears that between the piercing maxillae of the Hemiptera there are two fine channels, one dorsal in position through which the sap is sucked into the insect's pharynx, and the other ventral, through which the saliva of the insect is injected into the plant-cells where it acts on the dissolved sugar (Fig. 8, B). The proboscis is thrust usually between the cells of the cortex and reaches the vascular bundles, the bast-tissue (phloem) of which seems a favourite source of food-supply (Fig. 82); in order to obtain sap the insects usually pierce the individual cells where the saliva causes "plasmolysis and disorganisation of the cell-contents." It is of interest to notice that the same plant-tissues may be differently affected by the saliva of different species of sucking insect. Thus there are several kinds of plant-bugs of the capsid family which when immature feed on the juices of young growing apples in summer time. One of these (*Plesiocoris rugicollis*) has in recent years become an orchard pest, because the injury which it does to the fruit becomes apparent in autumn when the apples ripen, through cracking and deformation of the surface. Smith has shown that the saliva of *Plesiocoris rugicollis* alone among the capsid bugs has this definitely poisonous effect on the fruit tissues. Some sucking insects, by piercing the epidermis of plants, open a way for the invasion of bacteria and other minute organisms into the plant-tissues. Thus it is



believed that certain plant-bugs infect potato-leaves with "mosaic disease," and that the woolly aphids (*Schizoneura lanigera*) piercing apple-bark, facilitate entrance of the spores of *Nectria*, the canker-fungus. Among biting insects it may often be noticed that a strong-jawed creature such as a wireworm, by biting through the tough epidermis of a root or tuber, opens the way for hosts of frail springtails and mites to invade the soft internal tissues.

In the survey of the activities of social insects given in a previous chapter the specialisation in form and habits of bees (p. 225) in correspondence with the floral structures and products (nectar and pollen) which serve as the source of their food-supply was emphasised. Later, in discussing the evolutionary history of the insect orders (p. 343) it was pointed out that the rise and development of the flowering plants had been brought about concurrently with the specialisation of those groups of insects among the Hymenoptera, Diptera, and Lepidoptera that seek in blossoms for their food. The relations between such insects and flowers are among the most remarkable of associative features shown by living beings, and suggest irresistibly that the insects and the plants have grown, as it were, to fit each other in the course of their long histories. The adaptation of many flowers of diverse families to the visits of insects, so that the insects obtain nectar or pollen, and incidentally effect the cross-pollination of the flowers, as they pass from plant to plant in their search for food, has been a fascinating subject of biological study since the fundamental observations on the subject made by C. Darwin on orchids (1862) and other plants (1877), by J. Lubbock (1875) and by H. Müller (1878). It is unnecessary to repeat here details as to the pollination of orchids, arum, primrose, labiates, and many other plants set forth by those and subsequent writers, especially as the subject has been already discussed in detail in another volume of this series (M. Skene, 1925). It may suffice to recall summer hours spent in watching the visits of insects to blossoms: a humming-bird hawk-moth poised in air, with its wings

in rapid vibration and its long suctorial maxillae thrust accurately into the heart of some bell-flower ; a bee alighting on and depressing the lip of a snapdragon, crawling into the corolla which closes behind her, and then emerging, her back dusted with pollen some of which must adhere to the stigma of the next flower visited ; a miscellaneous assembly of Diptera, mostly drone-flies, on the flower-heads of some richly blooming composite, where the drone-fly constantly thrusts her proboscis, extended and flexed in rapid alternation, in and out of the yellow florets, pausing at intervals to clean the sucker from superfluous pollen by using her fore-legs as combs ; a large variety of much smaller Diptera on the white, flattened flower-heads of a roadside umbelliferous weed, attracted by the rank scent as well as by the large, conspicuous area presented by the expanse of white petals individually small. One cannot watch familiar sights like these without the thought that the insects and the flowers are fitted to each other as the eye to the light or the lock to the key.

Though all insects are dependent on plants directly or indirectly for their supplies of food, it is well known that there are some plants which are definitely destructive to certain insects. While the forms and appearance of flowers are adapted to attract such insect visitors as bees and Lepidoptera which effect pollination, there are often specially arranged barriers of hairs which guard the nectaries from the access of small Diptera and ants which could render no service in return for the nectar that they might obtain if admitted. Some plants—the “ Catch-flies ” of the Pink family, for example, species of *Lychnis* and *Silene*—have on the calyx glands that secrete a sticky fluid which entangle the feet of small insects as they seek to crawl upwards to reach the corolla ; unable to move they perish outside the unfriendly flower. Other plants possess more elaborate modifications by which they not only catch and kill insects but digest the nutritious parts of their bodies thus supplementing the food-supply as elaborated by green plants generally from inorganic substances. Of these

insectivorous plants, the Sundews (*Drosera*) are perhaps the best known among our British Flora, their leaves furnished with stout knobbed hairs, which, when an insect alights, bend over and hold it, while a "gastric" secretion is poured out over the victim. Many kinds of moorland insects are caught in the Sundew's deadly trap, and a grim illustration of the conflict involved in feeding is afforded by the small dragon-flies (*Agriionidae*) often to be seen on *Drosera* leaves; these creatures of prey, having captured and devoured many weaker insects, for the most part plant-eaters, are themselves caught and, so far as may be, assimilated by the Sundew. Even in the waters of pools and streams aquatic insects may be caught in the little pouches that are modified from portions of the divided leaves of the bladderworts (*Utricularia*) and serve to swell the food-supply of those submerged plants. Among tropical insectivorous plants the "Venus Fly-trap" and the various "pitcher-plants" are familiar to all students of this fascinating branch of our subject.

Not only these highly organised flowering-plants, but many lowly Cryptogams live in various ways at the expense of insects. The digestive tracts of bees and of many other insects harbour a great variety of bacteria which find nourishment in the partly digested food-products, and in some cases help incidentally to complete the digestive processes. Some of the bacteria harboured by insects are definitely harmful by inducing diseases in their hosts, such as those which cause the various types of "foul-brood" in hive-bees. The fungus *Empusa muscae* is often deadly to autumnal House-flies, as C. G. Hewitt (1914) and others have pointed out. The internal organs of the fly are completely destroyed by this fungus, and the dead insect is surrounded by a mass of white spores. A fly becomes infected when, from a spore settled among its hairs, a fungal filament (hypha) is extruded, pierces by solvent action through the chitinous coat and then, branching and penetrating throughout the internal tissues and organs, fills the fly's body-cavity with meshes of mycelium, whence there



finally penetrate to the outside the filaments that give rise to the spores (conidia) that are set free by thousands and millions. The elongate, conspicuous fructifications of fungi of the genus *Cordyceps* growing out of the bodies of caterpillars infected or killed by those organisms are among the well-known "curiosities" of insect relationships.

Insects are of great importance as a source of food-supply to predaceous animals of diverse kinds. Spiders of various families, differing in structure and habit, stalk-insects as they feed on plants, pursue and run them down in fair chase, leap suddenly from their lairs on unseeing insect victims, or set silken snares which appear cunningly woven to catch the feet of flies. Many aquatic insect larvae serve as food for fishes; mayfly are devoured in myriads at the season of their emergence by trout. Birds of many families take insects as their staple food at least during part of the year, rapid fliers like the swallows, martins, and swifts, seizing small insects on the wing as they swoop through the air, while such birds as tits, wagtails, and warblers search diligently for caterpillars feeding on plants or for aphids and scales sucking sap. Wading birds take toll of marsh-feeding grubs; rooks and gulls eat voraciously the root-feeding larvae of the soil. Even mammals do not all disdain insects as food. The American ant-eaters and the African and Oriental pangolins break into ants' nests and with their long tongues lick up the inmates. Bears raid the nests of wild bees for honey, and the badger of our own countryside often digs out wasps' nests (Plate VIII, B) and makes a good meal on the succulent grubs.

We must now consider a few of the immense number of examples of special life-relations which may be observed between insects and other animals. Many of these, directly bearing on methods of obtaining food, and on the comradeship between societies of insects and "guests," whether insects of diverse kinds or orders, or animals of other groups, have been described in previous chapters (pp. 248-52, 259-60). Here it may suffice to notice examples of insects

that live temporarily or permanently as parasites on or in the bodies of large animals and at their expense, and then examples of creatures, usually of minute size, which live as internal or external parasites of insects, or in very close association with them.

In a pasture on a summer day the grazing cattle are commonly surrounded by swarms of flies, mostly Diptera. Some of these belonging to the house-fly group are attracted by the odour arising from the skin, and lick up at intervals the drops of sweat and other surface exudations. The abundance of such flies attracts a number of worker wasps which, flying around the cattle, pounce on some of the flies and carry them off to feed the grubs in the nest. The beasts show considerable patience through the unwelcome attention of their insect visitors, but occasional or frequent lashings of the tail afford evidence of irritation. Besides the muscoid flies there may be seen various members of the blood-sucking tabanid family, provided with a battery of lancets, as previously described (p. 21, Fig. 7), for piercing the skin of the cattle in order to reach the desired food-supply. The smallish grey "cleggs" (*Haematopota*) alight on the beasts' hairs and inserting their stylets into the skin, proceed to draw at leisure their fill of bovine blood. To such attacks a calf or heifer responds by contraction of the cutaneous muscle so that the skin moves jerkily over the underlying tissue, and the clegg may be shaken off. The large breeze-flies (*Tabanus* and *Therioplectes*) have stronger piercers than the cleggs, and inflict wounds that may be regarded as painful. When a great *Tabanus* approaches grazing animals, its flight announced by a loud hum, the cattle often run about the field in agitation and apparent fear, as though they recognise in this insect a formidable foe. Yet it is known that these flies often vary their diet of blood by licking up juices from the surface of plants, and it is likely that many of them, like a large proportion of the gnats and mosquitoes of sparsely inhabited countries, never have in all their lives an opportunity of sucking blood. The larvae of *Tabanidae* do not feed in any way at the expense of cattle,

but prey on worms, molluscs, and insects that live in the soil or in water. The female flies lay their eggs in clusters on the leaves of plants or in other situations whence the grubs can easily reach the ponds or damp earth in which they live as hunters of their weaker companions in such situations.

While the Tabanidae and other groups of Diptera feed in their adult state as they have opportunity on the blood of mammals, there are many muscoid flies which, not themselves directly affecting the large beasts, have maggots which live as parasites of these. Reference has been made in a previous chapter (pp. 112-113) to the heavy mortality caused among sheep by the maggots of green-bottle flies (*Lucilia*) and allied insects, which lay their eggs on the wool, the larvae when hatched eating their way through the skin and into the flesh of the animals. This repulsive type of parasitism appears to have arisen from the carrion-feeding habit characteristic of blue-bottles and allied flies of the same family; an occasional laying of eggs on living instead of dead beasts having become largely habitual in *Lucilia* and the other European and Australian insects whose maggots feed in this way. Such parasitism is necessarily harmful and often fatal to the host-animal and must seem to many observers an example of disharmony in nature.

On the other hand, there are some well-known muscoid flies whose larvae are adapted in a wonderfully specialised manner to a parasitic life in the bodies of mammalian hosts. These, known collectively as the "bot-flies," have generally been regarded as forming a special family, the Oestridae. Several recent systematic students of the Diptera believe, however, that among them are representatives of two distinct muscoid groups, which having adopted similar modes of life have come by convergent evolution to similarity of form both in the larval and adult stages of the life-history. In a previous chapter (pp. 109-110) some account was given of migration through the bodies of cattle of the larvae of some members of the Oestridae, the warble-flies (*Hypoderma*), as affording examples of behaviour conditioned to some



extent by simple physiological reflexes, but with apparently purposeful reference to the course of the life-history of the insects. Some further details of the form and habits of these flies and their maggots may now serve to illustrate their adaptive relations with their hosts. The flies are hairy insects with sufficient resemblance to bumble-bees to suggest "mimicry," were it not that their habits are such as to give little hint of utility in their likeness to stinging Hymenoptera. They are on the wing from mid-May till early September—a succession of individuals, as the flies with aborted mouth-parts cannot feed and must be short-lived. The two species are largely seasonally isolated, *H. lineatum* appearing in May and June, *H. bovis* in July and August; thus together they have opportunity of egg-laying all through the warm weather. They fly in sunshine with a hum distinct though not loud, and at their approach the cattle run about in apparent terror, with their tails elevated—a remarkable and inexplicable fact as the flies can neither sting nor bite. Because of this effect of the flies on the cattle, the name "gadfly" has been applied to them as to the large Tabanidae already mentioned in this chapter. When a female warble-fly "strikes" at a beast the telescoped tail-segments are partly extruded and the eggs, held by the processes of the ovipositor (Fig. 35, C), are laid on the hairs, each egg being provided with a short stalk expanding into a grooved elliptical base which fits neatly astride the hair, and is secured in place by a maternal secretion which hardens to form a cement. It is interesting to note an apparently constant distinction between the two species of *Hypoderma* in their egg-laying habits: the larger eggs of *H. bovis* are placed singly close to the base of a hair, while the smaller eggs of *H. lineatum* are arranged in rows of seven to twenty along the middle region of a hair, their grooved bases in close contact (Plate II). Perhaps because the former species gets nearer to the beast's skin its attentions seem usually to irritate the cattle more than those of the latter, as S. Hadwen (1912, 1919) has observed. About four days after laying, the eggs are hatched, the larva being by

then developed, with its strong segmental spiny armature and its pair of relatively large and powerful mouth-hooks, diverging laterally with a sharp median process forwardly directed between them (Fig. 83). H. Gläser (1913) has described how the little maggot alternately draws back and thrusts forward the head-region so that the sharp point of the forwardly directed spine strikes strongly from within at the pole of the egg-shell, at length piercing it. Then the paired mouth-hooks come into play, tearing a slit in the end of the egg-shell, through which the maggot works its way out, the rows of backwardly pointing spines on the body-segments holding successively to the edge of the slit and preventing slips backwards. Out of its egg-shell at last, the little maggot crawls along towards the root of the hair, and taking advantage of the hair-follicle, begins to pierce and bite its way through the skin, disappearing completely in a few hours (Plate III, A). Entrance to the beast's body is thus made just wherever the eggs happen to have been laid by the mother-fly. The position of the eggs varies considerably but, as mentioned in a previous chapter (p. 109), they are always placed comparatively low, usually on the heels or hind-quarters, less often on the fore-limbs or flanks. The general course of their wanderings has already been described, upwards and forwards beneath the skin and through the tissues to the sub-mucous coat of the gullet where many may be found in the second and third stages from August to January, resting or wandering to and fro in the gullet-wall. The second-stage maggot (Plate II, D) is relatively slender, from five to ten times as long as the newly hatched instar, which it closely resembles in the form of its mouth-hooks and the spiny armature at the hinder end of its body around the tail spiracles. There are transverse rows of spines on the body-segments, which, though as large as those of the first-stage maggot, are far less conspicuous because more widely spaced. The mouth-hooks and spines, together with the complex musculature, enable the little larvae to carry out their extensive migrations through the tissues of the host-animal. The third-stage maggot of

Hypoderma, as recently pointed out by E. W. Laake (1921), though it resembles the preceding instar in general form, mouth-hooks and tail-spines, differs from it in the complete absence of spines on the body-segments, the surface of the cuticle being quite smooth. Nevertheless it wanders by devious ways, to the final position beneath the skin of the beast's back where the warble-maggots may be found in the third, fourth, and fifth stages from January until June, by which time most have become "ripe," although some belated individuals remain in the cattle until July or even August. The maggots pursue various paths in their journey, some taking a direct route backwards by way of the dorsal muscles and the vertebral canal, others travelling in the tissues of the diaphragm and thence working to the region of the back. Hadwen (1916) traced the course of one from the gullet to the margin of the diaphragm and thence through the intercostal muscles between two ribs to the neighbourhood of the backbone. The travels of these maggots through the body of the bullock or heifer, by various paths to a definite goal are surprising, and illustrate vividly the adaptation of parasite to host. It is certain, however, that a considerable proportion of the young larvae which, after hatching, bore into the skin, may lose their way in the tissues of their host and perish long before the attainment of their full growth. In the course of experimental work it was found that out of 187 eggs laid by a female *Hypoderma bovis* on the heel of a calf only 41 ripe maggots were developed in the succeeding spring.

Soon after arrival beneath the skin of the back the warble-maggots bore through the hide, thus establishing contact with the outer air for breathing and later emergence, undergo another moult (Plate XVI, A), and assume the fourth larval form. This is relatively stout with rows of spines on the ventral aspect of the body-segments and with conspicuous circular tail-spiracles directed to the air-hole through the host's skin (Plate XVI, B). The most remarkable change in this instar as compared with the earlier stages, is seen in the mouth armature ; as described by G. Phibbs



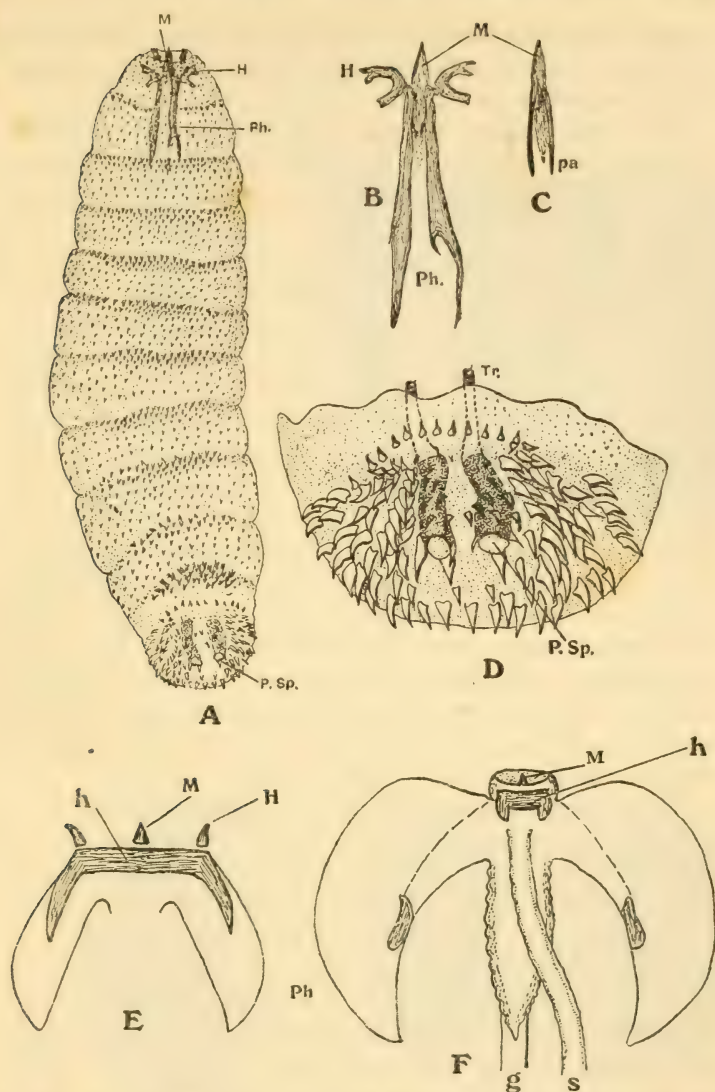


FIG. 83.—A, First-stage Larva of *Hypoderma bovis*,  $\times 100$ . B, C, pharyngeal sclerites (*Ph*), mouth-hooks (*H*) and median spine (*M*) formed by union of parastomal sclerites (*pa*),  $\times 250$ . D, hinder region of larva, *P.Sp.*, posterior spiracles; *Tr*, air-trunks.  $\times 250$ . After Carpenter and Hewitt (*Sci. Proc. R. Dublin Soc.* 1913, xiv). E, mouth armature of fourth-stage (penultimate) larva,  $\times 50$ ; F, of fifth-stage (final) larva,  $\times 25$ ; *H*, mouth-hooks; *M*, median spine; *h*, hypostomal sclerites; *g*, gullet; *s*, salivary duct. After G. B. Phibbs (*Irish Nat.* xxxi, 1922).

(1922) the paired hooks and the central spine are reduced to minute conical processes (Fig. 83, E); the larva has no further occasion to bore or migrate. The cuticle of the fourth-stage maggot is pale and comparatively feeble. When some weeks later the final (fifth) larval stage is reached, the mouth-armature is still further reduced, as the hooks are altogether wanting (Fig. 83, F). The cuticle is firm and tough, and most of the body-segments have transverse rows of strong spines on both the dorsal and ventral surfaces, as well as groups of spines on the lateral areas of the body. After the moult which ends the fourth stage the fifth-stage larva is pale, but as it ages it becomes darker in colour and when ripe assumes a grey or brown hue. In form it is stout, widest at the middle and tapering towards the rounded head and tail regions; at the latter the almost black, firm, spiracular plates are very conspicuous (Plate XVI, C). These may be seen through the hole in the host's skin, which is raised into a hemispherical prominence over the hollow swelling or tumour ("warble") in which the maggot during its two last stages lives and feeds (Plate III, C). The surrounding subcutaneous tissue and muscle undergo destructive liquefaction through the irritation and secretion of the parasite, which is thus able to secure by suction an abundant and nutritious supply of food.

The spiny armature of the ripe maggot enables it to work its way through the hole in the host's skin, as the armature of the young larva assists its emergence from the egg. The firm tough cuticle is adapted for the maggot's short life in the outer world, and becomes modified, as in muscoid transformations generally, into the hard puparium (Plate XVI, D) within which the imaginal structures are developed. About five or six weeks after the ripe maggot has worked its way out of the host animal's back, fallen to the ground, and sought shelter under a clod or stone, the fly breaks out of the puparium, and the female after pairing starts anew the yearly life-cycle by laying her eggs on the hairs of the cattle. It is interesting to notice how, in the seasonal adaptation of these insects to their hosts

# PLATE XVI



A



B



C



D

WARBLE-MAGGOTS (*Hypoderma*). A, Moult of 3rd stage cuticle revealing 4th instar. B, 4th stage larvae (dorsal and ventral aspect). C, 5th stage (final) larva of *H. lineatum*. D, Puparia of *H. bovis* (dorsal and ventral aspect).

To face p. 404.]

[T. Price & H. Pattison, photo.]





the larvae are sheltered in the bodies of the cattle through the autumn, winter, and early spring months.

The warble-flies and other Oestridae are in the perfect winged state elaborately organised Diptera, like the blood-sucking Tabanidae previously mentioned in this chapter. They fly after the animals, the former to lay their eggs, the latter to suck blood for food, and, their object accomplished, fly away again. When, however, the insect becomes in its adult stage definitely parasitic in its way of life, a tendency to degeneration is usually apparent, even though the adaptation to the host necessitates a degree of specialisation. Such conditions are well exemplified by the Hippoboscidae, a small family of Diptera among whose members can be observed degrees of specialised parasitism. The Forest-fly, *Hippobosca equina*, a common insect on the Continent and in parts of southern England, annoys horses by alighting on their bodies, clinging to their hairs and sucking their blood. Its feet carry strong-toothed claws as well as highly developed adhesive pads and complex feathery hairs, so that it secures firm hold of the coat of the horse on which it settles ; more than a hundred of these flies have been observed crawling or clinging on a horse's back or limbs, and it has been stated by E. A. Ormerod (1896) and others that the animal suffers more irritation from the insects' incessant movements over its body than from their blood-sucking activities. The forest-fly's wings are of normal length for its size but relatively narrow. In the allied *Ornithomyia avicularia* which attacks various birds the wings are still narrower, and in *Lipoptera hirundinis*, a well-known parasite of swallows, often found in their nests, these organs are reduced to short strap-like vestiges. The well-known " Ked " of sheep (*Melophagus ovinus*) with feet elaborately specialised for clinging, like those of *Hippobosca*, is altogether wingless. Various members of this family illustrate, therefore, the establishment of winglessness as an accompaniment of parasitism. It is of interest to notice among them a remarkable specialisation of life-history. Instead of laying an egg or giving birth to an early-stage

maggot, the female brings forth a ripe larva which quickly pupates ; by this means the preparatory stages of the normal insect transformation with their accompanying risks are largely eliminated from the life-history. It will be realised that the animals on which these insects live and feed, are such as afford through their family or social life-relations, opportunity for the passage of the parasites from one host to another.

There are two orders of wingless parasitic insects, allied to some of the winged groups that display the open type of wing-growth (Exopterygota) and undergo through their development a series of moults without any marked change of form. These are the Mallophaga (biting-lice) with mandibulate jaws, and the Anoplura (true or sucking lice) with highly specialised piercing and suctorial mouth. They all have very special parasitic relations with warm-blooded vertebrates, the vast majority of the Mallophaga being attached to birds and the small minority to mammals, while the Anoplura are found on mammals only. The Anoplura are blood-suckers, piercing the skin of their hosts to obtain food, while Mallophaga bite the feathers or hairs of their hosts, and eat the surface layers of the skin and its hardened secretions, sometimes causing such abrasion as to draw blood. In the Anoplura and the mammal-infesting Mallophaga the relatively short, stout foot has only a single strong claw, which in conjunction with a pad on the tarsal segment, clasps the hair of the host-animal ; these insect parasites therefore cling very closely. Their eggs are cemented to the hairs or feathers and the whole life-cycle is usually passed on the same beast or bird, though the habits of the host being often social, the insects may have opportunities of transferring themselves to fresh carriers. Each species of these parasites usually infects some definite host, and in most cases, it is impossible to discern any special reason for their slight but constant specific differences. Not infrequently, however, the same kind of mallophagan is found to live indifferently on several allied species of beast or bird. *Docophorus communis* has indeed been recorded from a



hundred different passerine birds of various families—larks, finches, thrushes, and others—inhabiting both Eurasia and America. V. L. Kellogg, in a highly interesting discussion (1913) of the Mallophaga and their hosts, points out that such distributional facts can be explained on the supposition “that the parasite-species has been handed down practically unchanged to the present . . . distinct bird species from their common ancestor of earlier days.” In contrast with the specific differences between the European and the American Coot or the European and the American Avocet, “the parasite of the common avocet or coot ancestor of the two present bird species remains unchanged, and is thus a single species common to the two geographically separated, never-meeting host species.” In many cases besides that of the *Docophorus* mentioned above, birds of distinct genera and even of distinct families harbour identical parasites. The most remarkable example of this is afforded by the flightless birds (Ratitae or Struthionies) of the great southern continents. On the South American “ostriches” (*Rhea*) live three species of *Lipeurus*, “one being found on each of the two host species and the other two on a third.” One of these *Rhea*-haunting biting-lice reappears on the true *Ostriches* of Africa, and another on an Australian Cassowary. The significance of these associations is astonishing, for it follows certainly that these three families of large flightless birds, so distantly related that their common origin has been by competent ornithologists denied and their likeness attributed to convergence, must be derived from a common stock, on which the two species of *Lipeurus* lived in mid-Tertiary times and have since then undergone no specific change.

Since insects of many and varied types live as parasites on large animals, it is not surprising to find that many minute creatures live on or inside insects, and such life-relations become especially interesting in cases where the insect-host serves as a living link between the other two organisms. The Mallophaga furnish a well-known example of this connection in *Trichodectes canis*, the biting-louse of

the dog ; in the body cavity of this insect as well as in that of the dog-flea (*Ctenocephalus serraticeps*) lives a larval parasitic worm (Cestode), and if the dog, irritated by the presence of lice or fleas bites at its own skin and swallows the insects, the cestode larva (cysticeroid or modified " bladderworm ") develops in the dog's digestive tract into the mature tapeworm *Dipylidium caninum*, from whose eggs are hatched the tiny six-hooked larvae which have opportunity to invade the bodies of the insects and there undergo the early stages of their life-history.

Students of the Trematoda or flukes, like the Cestoda, a class of flat-worms, find that an insect may be one in a chain of the hosts which successively harbour a fluke at some stage of its life-cycle. Thus a little tailed cercaria-larva which has developed in the body of a water-snail (*Limnaea*), may penetrate into the water-beetle *Ilybius fuliginosus* and encyst ; if the latter is eaten by a frog the cercariae thus swallowed will develop further into mature flukes (*Distomum cylindraceum*). Another trematode cercaria may migrate into the larva of a mayfly, a stonefly or a chironomid midge, and remain encysted until the insect-host has completed its transformation and acquired wings. Then in its aerial flight this insect may fall victim to a bat, within whose digestive tract the cercaria grows into the mature fluke *Distomum ascidia*.

The slender threadworms of the Gordius group make use of insects during the parasitic phases of their life-histories. The tiny larvae of *Gordius tolosanus*, as described by Von Linstow (1891) hatched from eggs laid in water, are provided with spines on the broadened head region, by means of which they bore into the larva of the alder-fly (*Sialis lutaria*), of a mayfly or of some other insect that is aquatic in its early stages, and come to rest in the muscles or the fat-body of the host. Here the Gordius larva shelters and feeds through the winter, and by the ensuing spring the insect-larva may have completed its transformation. If the mature fly containing the young Gordius is eaten by a ground-beetle (*Pterostichus*) or other predaceous insect,

it develops within this second host into the characteristic elongate, slender worm which after absorbing all the fat-body and other internal organs of the beetle, bores its way into the outer world to become mature in water or damp soil. *Gordius* has been observed to attain a length of over 120 mm. (about 5 inches) within the body of a *Pterostichus*, whose cavity may be almost choked with the parasites' closely packed coils. Long, slender threadworms of the *Mermis* group, somewhat like *Gordius* in aspect but belonging to the *Nematoda*, undergo their development and attain almost to their full size in the bodies of various beetles as well as those of grasshoppers and cockroaches. Cockroaches and other insects often harbour several kinds of *Nematoda* belonging to *Oxyuris* and other genera. A species of *Filaria*, encysted as a larva in the fat-body of the common Kitchen Cockroach (*Blatta orientalis*) becomes mature in the digestive canal of the omnivorous rat. The curious parasitic worms known as the *Acanthocephala* which live when mature in the intestine of vertebrates have several species whose larvae are parasites of insects. For example, the large fleshy grubs of chafers may be infested by larval *Gigantorhynchus gigas*; if such a chafer-grub be devoured by a rooting pig, the *Gigantorhynchus* will attain its adult condition in the pig's digestive tract.

The intestines of insects, like those of many other animals, are often inhabited by large numbers of unicellular organisms of the great group known as the *Protozoa*. Cockroaches harbour an assemblage of *Rhizopoda*, *Gregarinida*, *Infusoria*, and *Flagellata*, many of which appear to be simply parasites. *Gregarines*, *Clepsidrina blattarum* for example, are found as minute, intracellular parasites in the epithelium lining the cockroach's stomach; they grow, extrude from the host-cell, and becoming free in the gut-cavity proceed to the pairing of individuals which precedes division into gametes, conjugation, and the formation of resistant spores. Elongate *Flagellata* belonging to *Leptomonas* (Fig. 84, c) and allied genera often abound in the food-canal of *Hemiptera*, *Diptera*, and other insects. A point



of much interest recently established by the researches of L. Buscalioni and S. Comes (1910), and A. D. Imms (1919), is that many of the flagellate protozoa living in the intestines of termites (Fig. 84, *d*) are not parasites but symbionts, obtaining food for themselves and digesting it for the benefit also of the wood-eating insects which harbour them. It is only among termites of wood-eating habits that these protozoa abound; the wood, broken up by the mandibles and gizzard of a termite "is in a condition of minute fragments and particles," when it reaches the hind-gut, where, as Imms observes, "it gradually becomes taken up and absorbed by the numerous intestinal protozoa." There it undergoes digestion, and "when ejected from the bodies of the Protozoa much of it is . . . capable of being assimilated as food by the host termite." This "pre-digested" nourishment appears to be passed forward from the hind-gut into the termite's stomach for absorption.

Many of the Protozoa that live in insects are, like the tape-worms and threadworms already mentioned in this chapter, parasites which in the course of their life-cycles pass to and fro between insect and vertebrate hosts. This twofold relation of insects to other organisms has been the subject of numerous investigations during the last thirty years, and many of the ascertained facts are of high interest and great practical importance. Early in the last century European settlers in Africa found that imported cattle and other domestic animals bitten by Tsetse-flies (*Glossina*), a blood-sucking section of the muscoid group, were attacked by a fatal disease. David Livingstone's observations on this subject during his journey of 1850-52 are of much interest. After describing the distressing symptoms displayed by oxen and horses after being bitten by the Tsetse, he remarked that they "seem to indicate a poison . . . the germ of which enters when the proboscis is inserted to draw blood. The poison-germ . . . seems capable, although very minute in quantity, of reproducing itself." One cannot be certain that writing thus of a "very minute

poison-germ," the great missionary-explorer had actually in mind a microscopic organism, but his language suggests

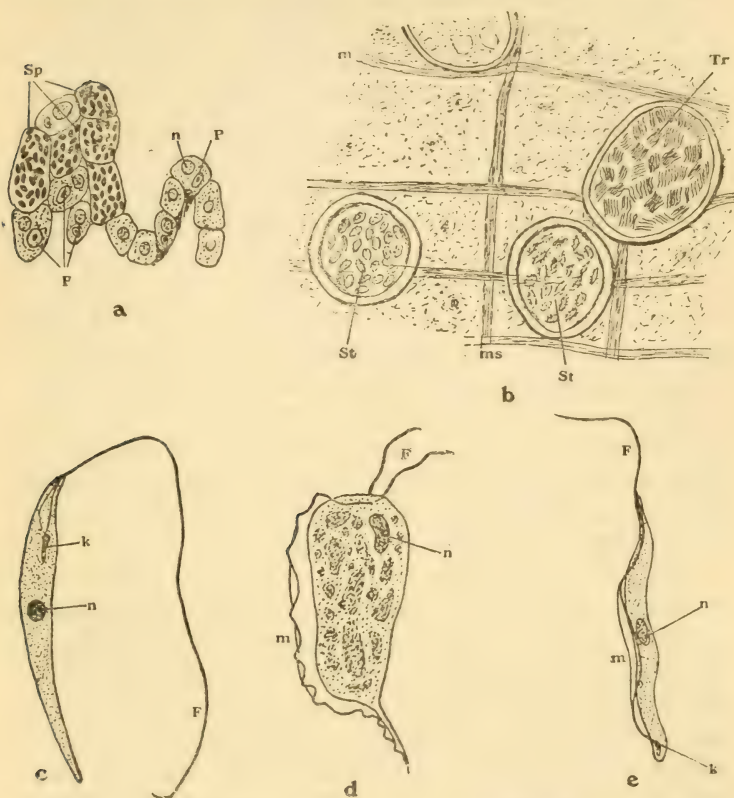


FIG. 84.—Parasitic Protozoa of Insects. *a*, Epithelium of stomach of Honey Bee infected with *Nosema apis*: *n*, nucleus of epithelial cell; *p*, *Nosema* (feeding-stage); *sp*, spores of *Nosema*.  $\times 700$ . *b*, Portion of crop ("stomach") of Mosquito (*Anopheles*) with cysts of malarial parasite (*Plasmodium*) containing sporoblasts (*St*) or developed sporozoites (*Tr*) (*m*, muscle bands).  $\times 700$ . After Nuttall (*Journ. Hyg.* 1901). *c*, *Leptomonas scatophagae* from fly *Scatophaga stercoraria*,  $\times 1750$ . After J. S. Dunkerly (*Proc. R. Irish. Acad.* xxxi, 1913). *d*, *Trichomonas termitis* from *Archotermopsis*.  $\times 1500$ . After A. D. Imms (*Phil. Trans. R. S.* 1919, ccix). *e*, *Trypanosoma gambiense* the "sleeping-sickness" parasite,  $\times 1500$  (*n*, nucleus; *k*, kinetocore; *f*, flagellum; *m*, membrane).

that conclusion, and more than forty years later D. S. Bruce (1895) described the flagellate protozoan (a species of

Trypanosoma) which is the actual cause of the deadly "nagana" disease in cattle and horses. A trypanosome when fully grown is a narrowly elongate cell, the locomotor whip-like process (flagellum) arising at the hinder end, is turned forward alongside the cell-body to which it is attached by a delicate "undulating membrane," and beyond which it projects as a kind of appendage (Fig. 84, e). Such a protozoan is well adapted for swimming through the blood-plasma, either in the blood-vessels of the beast or in the digestive tract of the tsetse-fly. Swallowed by the latter when drawing blood from one animal the trypanosome may be readily injected into another where it is "capable of reproducing itself" at an alarming rate. It is of much interest to note that *Trypanosoma brucei* is present in numbers in the blood of many African wild beasts, in which it causes no symptoms of disease. These creatures, accustomed to act as its hosts through countless generations, are immune to its effects, while closely allied animals imported into Africa from Europe succumb rapidly to the poisonous action of the tiny parasite's secretion.

In many cases of the infection of the large animals with Protozoan parasites, the blood-sucking insect serves simply as a "carrier" transmitting possibly many individual protozoans from one host to another. Frequently, however, the insect-host is of great importance in providing scope for some special and necessary phases in the parasite's life-history. For example, there lives in the blood of rats a parasitic flagellate known as *Trypanosoma lewisi* whose alternate host is the Rat Flea (*Ceratophyllus fasciatus*). When trypanosomes are swallowed with blood sucked into the flea's stomach, processes of cell-division begin which result in the production in the flea's hind-gut of a large number of parasitic forms, known as Crithidia, smaller than the typical *Trypanosoma* and without flagella. These migrate forward along the digestive tract, and injected from the mouth into the blood of other rats grow there into adult *Trypanosoma lewisi*. (See E. A. Minchin, 1912.)

Of all the Protozoa that live in the bodies of insects the



Sporozoa, to which belong the Gregarinida previously mentioned (p. 409), are perhaps the most remarkable because they display in the order Haemosporidia a specialised and complex adaptation to two alternate hosts—a blood-sucking insect (or other Arthropod such as a tick) and a vertebrate animal, on which that insect feeds. Many birds have Haemosporidia in their blood, each parasite when young invading a red corpuscle, growing and feeding therein until the blood-cell is broken down and the haemosporidian is set free in the plasma to divide into a number of daughter-cells, each of which can in its turn invade a fresh red corpuscle. After a number of such generations due to the division of the parent, individual parasites, free in the plasma, give rise to slender flagellate forms, while others assume a spherical shape and a passive habit. Further development can proceed only in the stomach of a gnat which happens to suck blood from the infected bird; in the insect's digestive tract the flagellate cells (which are really sperms) fertilise the spherical ones (which are eggs), and the resulting zygote becomes elongate or "vermicular" and penetrates into the stomach-wall where it greatly enlarges and undergoes extensive division so that ultimately a spherical cyst, filled with minute spindle-shaped motile cells or sporozoites, projects into the gnat's body-cavity. The sporozoites break out from the ruptured cyst and enter the salivary glands whence they may be injected into the blood of some other bird of which the gnat may make use to secure a meal. Thus there is a sexual phase of the parasite's life-cycle in the gnat, leading up to the production of multitudinous sporozoites, each of which, injected into the blood of a suitable bird-host can invade a red corpuscle and begin a series of asexual generations reproducing by multiple division ("schizogony"). It is noteworthy that the Sporozoa thus transmitted by alternate insect hosts have no firm-coated, resistant spores, such as in members of the class generally protect the sporozoites until they have been swallowed by the proper host. In these Haemosporidia, the active sporozoites (see Fig. 84, *b*) are passed into the

bird's blood along with the gnat's saliva, and protective spores are therefore needless.

Such spores are, however, a conspicuous feature in the life-history of some species of *Nosema*, minute sporozoan parasites, which belong not to the Haemosporidia but to another order, the Microsporidia ; two of these have attracted attention, as they infest respectively two insects domesticated by man—the Hive-bee and the Common Silkworm. *Nosema apis* (Fig. 84, *a*) is found in its various phases in the digestive tract of the Hive-bee and of other Hymenoptera, very minute cells, young individuals of *Nosema*, lying in the protoplasm of the bee's digestive epithelium, growing there, sometimes changing form and wandering about in the gut-cavity, or undergoing division so as to give rise within the bee's stomach-cell to a number of spores which may be set free in the intestine and passed out on to blossoms where other bees may lick them up and thus become in their turn infected. Bees harbouring large numbers of these parasites may be unable to fly and show other symptoms of disease, but it is exceedingly doubtful how far such conditions may be due to the presence of the parasites. *Nosema bombycis*, however, the microsporidian parasite of the silkworm (*Bombyx mori*) was clearly shown by L. Pasteur (1870) to be the organism causing the deadly disease known as pébrine, which threatened sixty years ago to destroy the silk industry in France. The caterpillars may swallow the *Nosema* spores with the skin of the mulberry leaves on which they feed, and the minute, active reproductive forms of the parasite may invade the ovaries and enter the developing eggs in caterpillars that will grow into female moths. Thus the embryo forming within the egg-shell is parasitised, and the young larva, hatched in an infected condition, is fated to be afflicted with the disease, which may be passed on from one generation to another. Such inherited transmission, relatively very rare among animals, is of great interest to the student of biology. It will be realised that disease incurred in this way is not, strictly speaking, hereditary, because its appearance in the

next generation is not due to the germinal constitution of the egg-nucleus, but to a perfectly distinct organism which is able to invade the egg before its maturation.

Some animal parasites much more highly organised than the protozoa, are found not within but outside the bodies of various insects ; these parasites, though far larger than the Protozoa, are necessarily small when compared with the insects that they infect. A large black dor-beetle (*Geotrupes*) is often found with the ventral region of the body and the bases of the limbs covered with little yellowish mites ; these are young forms of *Gamasus coleopterorum*, a member of a family of predaceous mites, the larger kinds of which pursue and capture small insects and suck their juices ; these tiny creatures can live in numbers as external parasites of a fairly large beetle. The water-mites (*Hydrachnidae*) mostly reddish in colour are well known to students of pond-life. The eggs are laid on water-plants and the six-legged larvae are parasitic on various aquatic animals, many species thus making use of the insects that share with them the freshwaters as a dwelling-place. Dragon-flies, aquatic Hemiptera like *Nepa*, *Corixa*, and *Notonecta*, and water-beetles are often found with numbers of hydrachnid larvae attached to various parts of their bodies. C. D. Soar and W. Williamson (1925) describe how the ventral surface of a large *Dyticus* may be "closely covered with larvae, the first comers attaching themselves to the under side of the head and succeeding attachments being behind these until the ventral surface is covered gradually from before backwards." This parasitism on insects is only temporary during the mites' larval stage ; when adult they feed at the expense of Arthropoda of another class, as they capture the small Crustacea known as "water-fleas." A mite *Acarapis apis* of the Tarsonemid family has been shown by Rennie (1921) to live and reproduce its kind in the large thoracic air-tubes of the Hive-bee, the mites gaining entrance through the spiracles, pairing and laying their eggs in the tracheal cavities. The walls of the air-tubes become discoloured through the piercing and sucking



action of the feeding mites, which may multiply to such an extent that they choke the cavities. Many bees thus infected lose their power of flight, and the "Isle of Wight disease," of which this inability is a conspicuous symptom, is now generally ascribed to *Acarapis* rather than to the *Nosema* mentioned above. It is easy to believe that the



FIG. 85.—Water-scorpion (*Nepa cinerea*) with small bivalve mollusc (*Sphaerium*) grasping its hind foot.  $\times 2$ .

damage and obstruction which these mites cause to the thoracic air-tubes may disturb the action of the wing-muscles by reducing their supply of oxygen; nevertheless some bees with a heavy infestation are able to fly very well, so the subject clearly calls for further investigation.

Besides the mites just described that are parasites, other members of the same order may be found attached to the bodies and legs of insects, flies, for example, not that they may suck food, but that their race may have the advantage of wide dispersal. The Tyroglyphidae

are a family of mites well-known to many persons, through the abundance of one or two species in cheese and stores of meal and hay. In their life-history there is a curious nymph-stage known as the hypopus—a form with flattened firm-coated body, beneath which the slender legs are inserted close together, being provided with sucker feet by means of which the little creatures maintain attachment to the flies or other insect-carriers on which they take opportunity to fasten. The sudden apparently inexplicable appearance of swarms of Tyroglyphi in a store of meal is due to the transport of hypopus-nymphs which, leaving hold of their fly carriers,

drop into the rich food-supply, complete their growth, and when mature increase and multiply at an alarming rate. Members of another order of Arachnida, the Chernetida ("false-scorpions"), also are often carried relatively long distances by flies to whose feet they cling with their small but conspicuous "pedipalps" which resemble in their form the pincers of a miniature lobster. It is also worthy of notice that insects take at least a subordinate part in helping the dispersal of creatures belonging to a very distinct group of animals, the Mollusca. Some interesting examples of such association are given by H. W. Kew (1893), and the majority of them refer to the carriage of freshwater molluscs by aquatic insects which are able to fly and thus carry the shell-fish from one pond or stream to another. Thus species of the bivalves *Sphaerium* and *Pisidium* have been found clasping, between the margins of the two valves of the shell, the foot of the water-scorpion (*Nepa cinerea*, Fig. 85) or the large water-beetle *Dyticus marginalis*, while these insects were flying through the air. Water-snails and the little fresh-water "limpet" (*Ancylus fluviatilis*) also can obtain aerial transport by crawling on to the elytra of water-beetles and adhering there by the "sucker" action of the foot; in this way new ponds and streams can be colonised by these molluscs and the range of their species extended. In such and in numberless other ways do insects come literally into close touch with other creatures, and in the course of their usually brief lives take their share in weaving the vast intertwined complex of vital connections that has been well named the "web of life."

## CHAPTER XIV

### INSECTS AND MANKIND

AFTER the preceding summary account of the bionomic relations between insects and other creatures, it seems fitting to dwell at the close of this book on some of the connections by which insects are in diverse ways, linked with the complex life of man, who, spread in his various races over the surface of the earth, is everywhere in touch to some extent with the world-wide hosts of insects. We have noticed many examples of insects that feed on plants cultivated by man as sources of his supply of food or clothing, of others that live as parasites on or in the bodies of his domestic animals, of others again which obtain the most unpleasantly close contact with himself as they feed by sucking his blood, and possibly leave therein minute organisms to induce serious or deadly disease. Man, as he seeks to fulfil his destiny to "replenish the earth and subdue it," finds that his progress is continually checked and sometimes arrested by "a thousand insect forms," individually small and feeble but collectively powerful, so that to the human pioneer a swarm of flies may prove an obstacle more formidable than "a lion in the path." On the other hand, the hive-bee, the various silkworms, the lac insects, are themselves domestic animals of no small utility, and in many aspects of the form and life of insects men find still, as they have found in the past, abundant material for fascinating and profitable study.

We have already seen that there is mutual action between insects and mankind in their food-gaining activities ; the



practice of agriculture and gardening, by crowding together on a comparatively small area of land enormous numbers of plants of the same kind, cannot but lead to rapid increase in the numbers of those insects of the district which can feed on the cultivated plants (see pp. 111-112). Thus cultivation tends to incite various insects to become pests, and then the cultivator finds it needful to take measures for the slaughter of the pests on a large scale. Similarly the shepherd and the cattle-owner collect in a restricted area flocks and herds of animals of the same kind, whose large numbers and ready accessibility must tend to abnormal multiplication of parasites of all groups. It is right that men, annoyed by insect pests, should remember to how great an extent the troubles that beset them are the direct consequence of their own actions.

As an example of an insect which in recent years has become a factor of great importance in human industry on several continents we may take the Mexican Cotton Boll-weevil (*Anthonomus grandis*). This small, long-snouted beetle (Fig. 86), never more than 4 mm. ( $\frac{1}{6}$  inch) long, and often much less, is a native of Mexico. In 1892 it crossed the border of the United States, appearing in the far south-western corner of Texas, along the Gulf coast. Thence its advance has gone on, sometimes at the rate of fifty miles a year, and it has now spread into Louisiana, Tennessee, Arkansas, Alabama, Georgia, Florida, and the Carolinas, thus over-running nearly the whole "cotton belt" in the course of some thirty-five years. The female beetles after hibernation bite small holes in the buds or the flowers and lay their eggs therein, the grubs feeding in shelter or concealment and pupating within the blossom or the capsule ("boll"). The beetles, after emerging from the pupal coat, continue to feed for weeks or months, so that the damage done to the crop in all stages of the insect's life-cycle is very heavy, though it has been computed that in the northern parts of its range, only about 2 per cent. of the beetles survive the winter. The annual money loss due to the ravages of this insect has been estimated at £50,000,000, and the President

of the New Orleans Cotton Exchange declares that "national prosperity is threatened by the ravages of this insect."

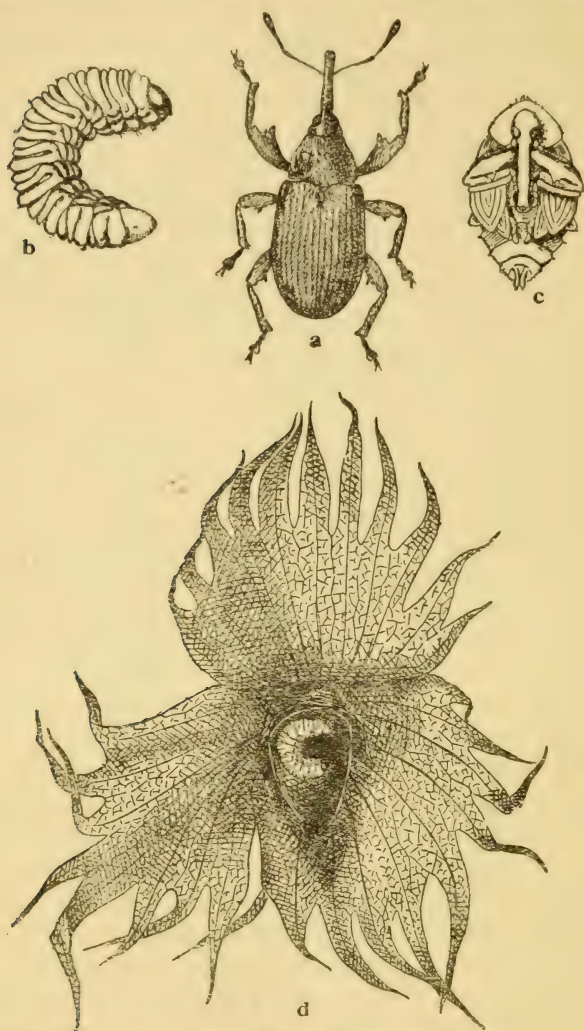


FIG. 86—*a*, Cotton Boll-weevil (*Anthonomus grandis*), Mexico; *b*, larva (side view); *c*, pupa (ventral view),  $\times 5$ ; *d*, cotton "square," showing larva feeding. Natural size. From W. D. Hunter and D. R. Coad (U.S. Dept. Agr. *Farmers' Bull.* No. 1329, 1923).

Arsenical sprays are used on a vast scale for the destruction of the beetles, the operation of spraying being frequently carried on from aeroplanes flying over the cotton fields, and an indirect result of the Boll Weevil's activity is that the price of arsenic has risen during the last ten years from £19 to £62 a ton, and that a number of Cornish tin-mines disused for years because tin ore no longer paid for raising, have now been re-opened for the sake of the profits derivable from the arsenical "by-product."

Though the Southern States of North America form still the greatest cotton-growing district in the world, other countries are coming into prominence as cotton-producing centres; among these Egypt, the Sudan, and Uganda are now noteworthy. In Africa and Asia the most serious cotton-pest is a caterpillar known as the "Pink Boll-worm," the larva of a small moth *Pectinophora gossypiella*. The moth lays her eggs on the blossom and the caterpillar bores in, feeding on the developing boll, and making its way into the seed before pupation. According to H. M. Lefroy (1923), 17 per cent. of the Egyptian cotton crop is destroyed by this insect, and its ravages have cost that country about £50,000,000 during the last fifteen years. The insect has been introduced into the West Indies and Tropical America, and the authorities of the United States are naturally eager to prevent its establishment in their cotton belt. From the summary of the life-cycle it will be realised that the wintering larvae may be readily introduced in seed; it is not surprising that Egyptian cotton seed has been forbidden entry at American ports, and that cargoes have on occasion been destroyed. Such facts as these demonstrate the importance now attached by the Governments of many great countries to the control of insect pests. Nearly all national departments or ministries of agriculture have well-organised entomological services the publications of which, with their detailed accounts of the life-histories and habits of injurious insects, and instructions as to methods of killing the creatures or preventing their ravages, prove that insects have forced themselves on the serious attention of civilised mankind.



The study of Economic Entomology and the recognition of its importance have advanced with the increase of knowledge as to the part played by insects as enemies of cultivated areas in almost all parts of the world. In our own islands the pioneers of economic entomology were enthusiastic amateurs like John Curtis (1859) and E. A. Ormerod (1877-1901). Now the subject is being systematically studied in the official laboratories of the Ministry of Agriculture, in the famous research institute at Rothamsted, and in connection with the faculties of science in most British universities. It is, however, on the great Continents, and especially in the tropics, that insect pests present the most serious problem to the cultivator. Through the activities of the British Imperial Bureau of Entomology and the authorities of the overseas Dominions, Colonies, and Protectorates, increasing attention is being paid to the importance of insects in relation to tropical agriculture and forestry, as well as to the entomological aspects of disease and preventive medicine which will be discussed later in this chapter. Most of the European Governments now show by their action a recognition of the importance of Entomology both in their home countries and in their tropical possessions. It must, however, be admitted willingly and gratefully that the United States of North America first taught the world how to deal on a large scale with insect pests. In the New England States entomological reports were officially published eighty-five years ago, and it is over seventy years since the inception of the world-famed Federal Bureau of Entomology at Washington. The practice of economic entomology requires not only a knowledge of the structure, life-histories, and habits of insects and their relations to their plants on which they feed : in the composition and application of dressings and spray-fluids for destroying the pests, problems of technical chemistry and the action of poisons—whether “stomach-poisons” like arsenical compounds to be swallowed by biting insects, or “contact poisons” like nicotine or paraffin to be absorbed by sucking insects—have to be taken into account. The subject is therefore one in

which co-operation and team-work become increasingly necessary to success.

Of special interest from the biological point of view are the many cases in which some insect deliberately or unwittingly introduced by human agency into a new country, has there become a serious pest on the farm or in the orchard or forest, and the subsequent attempts to naturalise in the invaded territory some imported natural enemy of the destructive insect so as to bring about the reduction or extermination of the latter. The classical example of this line of practice is afforded by the introduction forty years ago into California of a mealy-bug or "fluted scale" (*Icerya purchasi*) which increased and multiplied and attacked citrus groves so violently as to threaten destruction to an important industry. When the native country of the *Icerya* had been determined as Australia, a study of the insects of that region which prey on it in its homeland was inaugurated under the direction of C. V. Riley (1888), with the result that a ladybird-beetle (*Vedalia cardinalis*), selected for importation in quantity to California, exterminated the noxious fluted scale.

Among the injurious insects taken into North America from Europe the "Gipsy" Moth (*Porthetria dispar*) has become famous. Specimens were imported into Massachusetts in 1868 with the intention of using industrially the silk spun by the caterpillars. A number of insects escaped into the open country and the species, being easily spread by flight of the moths and wind-carriage of the young hairy larvae, has become a serious pest in the parks and gardens of New England. Much attention has been paid by American entomologists to the Hymenoptera and other insects that live as parasites on the "Gipsy" caterpillars, and many of these have been imported into New England in the hope, as yet unfulfilled, that some of them might exterminate the American colony of *Porthetria dispar*. But partially successful economically, this effort has added largely to our knowledge of the relations between the "Gipsy" and its predaceous and parasitic enemies (L. O. Howard

and W. F. Fiske, 1912). It is remarkable that this moth which has become a pest across the Atlantic during the last fifty years has within the same period completely died out as a native species in Great Britain. A remarkable recent success in acclimatising the parasitic enemy of an injurious insect has been achieved by R. J. Tillyard (1926), who has introduced from North America the chalcid *Aphelinus mali*, in order to keep in check *Schizoneura lanigera* the Woolly Aphid of the apple, brought into New Zealand years ago and established there as a pest "almost unbelievably virulent." After overcoming its first southern winter the *Aphelinus* has become so well established in its new home that "the woolly aphid is now under satisfactory control," and consignments of the parasite have been passed on to carry out similar beneficial work in Australia.

Among the insects that are especially liable to transport from land to land by unwitting human agency are those which live as "messmates" in dwelling-houses and stores, eating various foodstuffs provided by man, and finding in many haunts such shelter and warmth that they can, even if they come originally from tropical regions, survive and multiply amid suitable surroundings in cooler countries. Many insects of this associative group are, as might be expected, common on shipboard. In a previous chapter (p. 269) attention was called to the flattened body-form of cockroaches, making it as easy for them to shelter in the crevices of a dwelling-house as under bark or among fallen leaves in a forest. The Common Cockroach (*Blatta orientalis*) of our kitchens is, as its name implies, a native of the eastern tropics; it has now been established in Europe and Britain for more than a century, and in many districts its spread from larger towns to country villages may be traced; it seems, not by violent combats but by effective competition, to drive out from places which it invades that much older home-mate of European man, the House Cricket (*Gryllus domesticus*). The smaller and paler German Cockroach (*Blattella germanica*), a later



immigrant to Britain than *Blatta orientalis*, is said to supersede its larger, darker relation in many habitations. Certainly it is often present in swarms in the kitchens of old town dwellings, and in or under the cages of monkey-houses in menageries. The large brown American Cockroach (*Periplaneta americana*), whose original home was in warm transatlantic countries, is now often abundant on ships and in the sheds of docks and wharves; it may also be found in greenhouses, at times in company with its close ally *P. australasiae*, introduced from far Eastern tropics with imported plants.

Man's insect messmates comprise quite a number of small beetles that live in grain, flour, and other foodstuffs, and often increase in numbers so as to become serious pests. The beetle *Tenebrio molitor*, with its elongate brown larva the "mealworm," is found throughout the world in stores of cereals; the grubs pay some small compensation for their depredations by themselves serving on occasion as provender for pet birds. Two smaller "Flour Beetles," *Tribolium ferrugineum* and *T. confusum*, belong to the same family as *Tenebrio* and live in much the same way. Stores of grain as well as ship-borne cargoes are often infested with two small weevils, *Calandra granaria* and *C. oryzae*. During the Great War of 1914-18 the damage done by these and other food-devouring insects became so serious that in view of the shortage of supplies, a special government commission was appointed to inquire into the ravages of those insects that must be regarded as pests in warehouses and on board ship. The common little beetle *Anobium paniceum* which feeds in great variety of stored foodstuffs is often known as the "biscuit weevil" because of its destructive action on ship's biscuits, though it is systematically far removed from the true weevils (Curculionidae), being a member of the Clavicorn family Ptinidae. Various beetles of this family have become established as messmates in human dwellings and store-houses feeding not only on edible grains, meal, and dried fruits, but on drugs (including poisons such as opium,

belladonna and pyrethrum), cayenne pepper, and other apparently unpromising materials. One species, *Lasioderma serricorne*, a native of North America, indulges, according to G. A. Runner (1919), in all this wide range of feeding habit, but it has lately become increasingly notorious as the "Tobacco Beetle," as it has tended more and more to specialise on the prepared products of that plant, which is even by its human devotees not generally classed as nutritious. *Lasioderma* feeds indifferently on "cured leaf tobacco, smoking and chewing tobacco, snuff, cigarettes, and cigars." Through the closely rolled dried leaves of the last-named articles of luxury the whitish soft-coated grubs of the insect bore their way, and the adult beetles, their transformations complete, come out at the surface through neat circular "shot-holes." It is reckoned that through such damage to cigars a sum approaching £50,000 is lost yearly in the Philippines alone, and £5,000 was reported as the annual loss due to the beetles, suffered by a large tobacco business in the United States. Another firm had to discontinue the production and export of cheap cigars worked up from "scrap tobacco," because, through the destructive action of the beetles, a large proportion of the shipments were returned, though at the inception of this department of the business the profits made by it had amounted to \$7,000 a year. It is evident that the constant transport of a widely used commodity, such as tobacco and its products, must facilitate the extension of any insect that feeds on these substances, and the great masses of material housed in a confined space favour the creatures' rapid multiplication. With stored products as with field-crops, the actions of man himself tend to induce such quick reproduction of adaptable insects with plasticity of behaviour that they inevitably become pests. Then civilised man seeks to re-act to the loss that he suffers by attacking the destructive insects with all effective weapons from the armoury of modern science; and expensive machinery or apparatus is installed in order that thousands of little beetles and their grubs may be frozen under cold-

storage conditions, roasted by dry heat or scalded with steam, poisoned by fumigation with carbon disulphide or hydrocyanic gas, or killed by exposure to powerful Röntgen or ultra-violet rays.

The Ptinidae, as already mentioned, include many species commonly found in human dwellings, and among these some that feed on wood are of special interest. Probably before the advent of man the insects now known as the Furniture Beetle (*Anobium striatum*) and the Death-watch (*Xestobium tessellatum*) lived in old tree-stumps, having become adapted to feed on wood long dead and too dry for the sustenance of most boring insects. From such habitations it was natural to migrate as occasion offered, into wooden articles in houses or into the timber used in the construction of the habitations themselves. Thus we find chairs, tables, and other articles of furniture bored internally and with little circular holes at the surface that fit accurately the almost cylindrical form of the beetles as they emerge. Or the beams of wonderful and valuable oaken roofs like that of Westminster Hall become so badly damaged by generations of *Xestobium* carrying on their activities through centuries that the structure can only be saved from collapse by complete renewal of some parts and drastic treatment of others. A curious incidental result of the association between these beetles and mankind is the imitation by makers of sham antique furniture of the "shot-holes" which in many truly ancient chairs and tables witness to the former presence of families of *Anobium* inside their legs and frames. Not that such genuine scars in timber are by any means a certain indication of the venerable standing of the piece that shows them; they are often apparent enough in the cheap products of the modern "complete furnishing" factory. The name "death-watch," long ago applied to *Xestobium* and other timber-feeding beetles of the family, is well known to be due to the regular tapping made by the beetles with their mandibles on the walls of their galleries; such tapplings were naturally noticed by night watchers at bedsides of the sick and dying,



and as the cause was unknown the sounds were connected in the mind of the listener with the forebodings of sad and anxious hours.

Great as may be the damage caused to wooden articles and structures by these beetles in the temperate regions of the world, the ravages in the warmer countries of the termites ("white ants") owing to their timber-eating habits are far more serious than any due to insects of our northern countries. This is a result of the alarming rapidity with which a community of termites can eat a strut, a beam, a large piece of furniture, or several thick volumes into a labyrinth of burrows, and as the innate reaction of these insects is to shun the light, they may carry on their destructive work unobserved until the timber that shelters them collapses in hopeless ruin. Travellers in all parts of the tropics have true tales to tell of buildings, goods, and furniture apparently destroyed in a day or two, and a striking example is afforded by H. M. Lefroy's record (1923) of "the wood skids and frame of the aeroplane attacked in one night's halt" during the "Cairo-to-Cape flight" of a few years ago. The access of termites to the wooden parts of buildings is rendered easy wherever timber is sunk in the soil through which they migrate; and the use of concrete and brick foundations is to some extent a safeguard against the insects' ravages. Yet they often come up from the ground, covering their tracks by the construction of earthen tunnels, and it is on record that they "have actually bored through cement and lead" in their search for suitable feeding-grounds in wood.

In the preceding chapter several examples were mentioned of blood-sucking insects which act with the back-boned animals as alternating hosts or carriers of some microscopic parasitic organism, a bite by the insect drawing the parasites from or injecting them into the vertebrate whose blood is sought as food. Many minute organisms which have such life-relations with insect-hosts are transferred by them into or from human blood; thus certain insects are of the most serious importance in transmitting

the causal organisms of various human diseases. The demonstration and recognition of this dangerous connection between insects and mankind have proved a noteworthy scientific achievement of recent years, and "medical entomology" has become a fascinating subject of investigation at which the physician, the bacteriologist or protozoologist, and the student of insects may work in fruitful comradeship.

Just as the African Tsetse-fly *Glossina morsitans* transmits to cattle and horses the protozoan *Trypanosoma brucei* that causes "nagana" disease (pp. 411-412), so another species of Tsetse, *G. palpalis*, is the carrier and transmitter of *Trypanosoma gambiense*, which in man, migrating from the blood into the central canal of the nervous system, gives rise to the fatal disease which from its characteristic symptoms is known as "sleeping-sickness." The story of the discovery by which these facts have been established during the present century is well told by Hale Carpenter (1920). The *Trypanosoma* was first detected in Gambia in 1901 by Forde, who found it in the blood of an English patient displaying febrile symptoms, and the nature of the blood parasite was determined the next year when Dutton had opportunity of examining the patient in Liverpool. Then, in 1903, Castellani demonstrated the presence of *Trypanosoma gambiense* in the cerebro-spinal fluid of native Africans afflicted with sleeping-sickness, a disease long prevalent in the western part of the continent, always fatal, and though attacking large numbers of people, not appearing as an epidemic to the destruction of a high proportion of the inhabitants. It was in Uganda, in East Central Africa, that the disease appeared as an alarming threat to the health and survival of a great community. Dr. A. Cook, of the Mission Hospital at Mengo, recognised the disease in 1901 as a new and mysterious outbreak, for by the end of that year two hundred Baganda had died and thousands were affected, while in 1906 the Governor of the Protectorate reported that during the preceding five years "the total mortality from this scourge had considerably exceeded

200,000." The researches of Bruce, Castellani, and their colleagues demonstrated *Trypanosoma gambiense* (Fig. 84, e) as the causal organism of the disease, and *Glossina palpalis* as its alternative insect-host. Within the digestive tract of the tsetse, the trypanosome undergoes a distinct phase of its life-cycle with a result that after a few days of feeding on trypanosome-infected blood, a tsetse becomes non-infective and remains so for several weeks, until this developmental phase is completed; then members of a fresh brood of the *Trypanosoma* are ready to pass into the blood of human beings whom the fly may bite, and when it has thus "acquired the trypanosome the tsetse can infect for the rest of its life." Yet other creatures enter into this dangerous association, for it has been proved experimentally that monkeys can be infected with the *Trypanosoma*, and one of the "harnessed antelopes" (*Tragelaphus spekei*), as well as other kinds of African "big game," may serve as "natural reservoirs" for the deadly parasitic Protozoa.

There are many features of interest in the connection between the peoples of Africa, the tsetse-flies, and their parasites. Europeans are rarely afflicted with sleeping-sickness, because being more completely clothed than the Africans they are less exposed to the attacks of *Glossina*. The deadly incidence of the outbreak in Uganda is believed to have been due to the introduction of the fatal strain of *Trypanosoma* into a new district where the population, entirely unused to it, had acquired no degree of immunity, while the alternative insect-host was a fairly abundant member of the fauna. The introduction of the trypanosome seems to have been brought about by an increasing volume of traffic, commercial and military, during the last thirty years from the West Coast up the Congo basin to the great lakes of Eastern Central Africa. Like other species of *Glossina*, the female *G. palpalis* gives birth to a full-grown maggot which has the habit of burrowing into loose dry soil in shady places for immediate pupation. As a result of this habit, it is found that the tsetse pupae abound on the shores of the lakes, including islands, where forest or bush



grows down towards the margin of the water, and it was the island population of the Victoria Nyanza that suffered most severely in the Uganda outbreak of sleeping-sickness. Nothing short of the removal of the remnant of the lakeside population from the regions serving as breeding-haunts for the flies succeeded in staying the epidemic. Attention is now given to clearing the vegetation so as to make localities unsuitable for breeding, and attempts have also been made to provide areas with well-aired loose soil so as to attract female *Glossina* to deposit their larvae there; then the entomologist searches the ground diligently for the discovery and destruction of pupae. It is remarkable that a form of sleeping-sickness prevalent in Nyassaland is due to another species of *Trypanosoma*, *T. rhodesiense*, the alternative insect host of which is not *G. palpalis* but *G. morsitans*, the tsetse-fly which transmits the parasite of nagana to cattle and horses.

The tsetse-flies are entirely confined to the tropical regions of Africa, but there are few parts of the world in which some blood-sucking insects are not possible agents in the spread of human disease, and most of these belong to the Diptera or two-winged flies. Perhaps of all the various families of this order whose members may be deadly to mankind, the Culicidae, which comprise the typical gnats or mosquitoes, are the most important because the minute parasites harboured by various types of such insects are the causative organs of serious diseases, some of which are among the most fatal known to medical science. Of these the species of *Plasmodium*, *Haemosporidia* which in human blood give rise to the various types of malaria or ague, have attracted especial attention. The life-cycle of one of these *Plasmodia* in its alternating mosquito and bird hosts has been described in the preceding chapter (pp. 413-414), and the parasites of human malaria have a closely similar life-history, undergoing asexual reproduction in human blood by multiple division, and passing in the digestive tract of the mosquito, through a sexual phase which results in the production (Fig. 84, *b*) of a relatively large cyst

whence the minute active sporozooites escape into the insect's body-cavity and enter the salivary glands, so that they can be injected into the blood-stream of some other human victim of the mosquito's bite. There is, however, a constant and noteworthy difference in the culicid hosts of

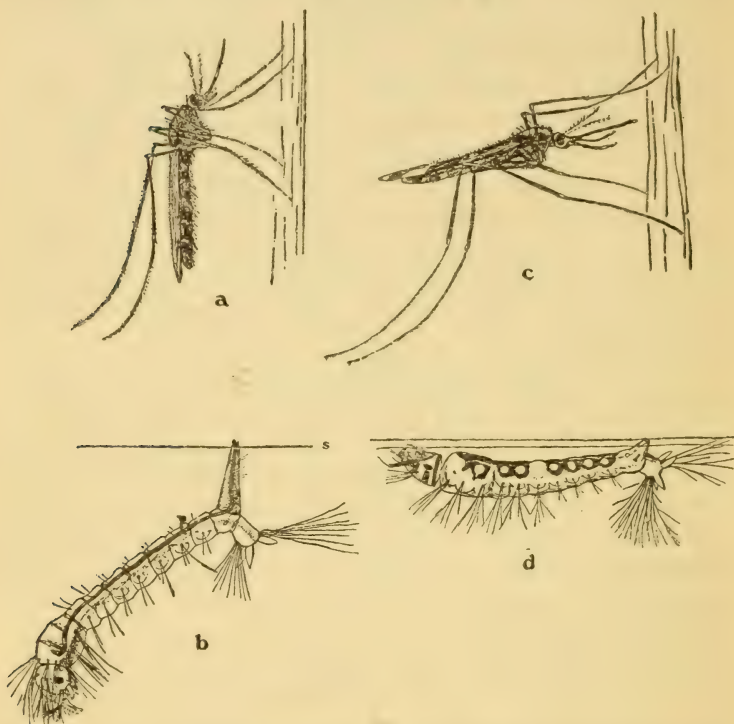


FIG. 87.—*a*, Culicine Mosquito and *c*, Anopheline (females) in resting position; *b*, larva of *Culex* and *d* of *Anopheles* showing suspension from surface film.  $\times 8$ . After L. O. Howard (U.S. Dept. Agr. Ent. Bull. 25).

the Plasmodia affecting respectively man and bird-hosts. In the case of the latter the insect is an ordinary female gnat of the culicine section of the family, distinguished by the palps being very much shorter than the sucking and piercing proboscis (Fig. 87, *a*). After R. Ross (1900) had demonstrated the part played by the species of *Culex* in

transmitting the sporozoites of the bird-infesting Plasmodia, he failed to obtain from experiments with those insects similar results as to the parasites of human malaria; later it was shown that these can undergo the sexual and sporulation phases of their life-cycle only in female Culicidae of the Anopheline group, whose palps are nearly as long as the proboscis (Fig. 87, *c*). It was thus proved that the spread of malarial disease is dependent on the association of infected human subjects with a definite section of the mosquito family.

The conclusion that these diseases, so serious and so frequently fatal as they are wherever prevalent, can be transmitted only by means of the bite of an infected anopheline mosquito, is of the very highest importance in preventive medical practice. The use of mosquito-nets or other means that may prevent the insects from sucking human blood (which they seek to do by night), and the elimination in the neighbourhood of towns and settlements of pools or reservoirs of stagnant water in which mosquitoes lay their eggs and where their larvae (Fig. 87, *b*, *d*) and pupae live, have proved effective safeguards in many districts once considered hopelessly unhealthy. It is an immense advantage when causes of disease are known which indicate the possibility of precaution. The term "malaria" suggests the belief that these diseases were caused by "bad air," the damp exhalation of marshes. It is now known that the marshes are dangerous because they serve as breeding-grounds for blood-sucking insects which act as alternative hosts of the micro-organisms actually causing the disease. The Roman Campagna was for long notorious as one of the most malarial districts in the world; within the last thirty years it has been experimentally shown that perfect immunity may be secured by sojourners there if they take precautions, by surrounding themselves with nets, to avoid being bitten by mosquitoes. The anopheline section of the Culicidae, whose members alone act as hosts of the malarial parasites, are represented in Great Britain and Ireland by three species which are widespread and in some seasons abundant.



Malaria was formerly a common and dangerous disease in England well known to physicians as "ague"; it was especially prevalent and indeed epidemic in the fen district of the eastern counties and the marshy regions of the Thames valley and the Channel coast. G. H. F. Nuttall and his colleagues pointed out (1901) that the British species of *Anopheles* are much more frequent in these localities than in western and northern districts. It appears that malaria or ague ceased to be an epidemic disease in England about the year 1860. From the ascertained facts Nuttall and his fellow-workers conclude that the former distribution of the disease was "not a matter of the geographical distribution of *Anopheles* as much as of their numerical distribution." The anopheline population became much reduced by the drainage of fens and marshes, while the human population of these districts was reduced by emigration into cities or overseas, and the use of quinine in medical treatment tended to destroy the *Plasmodia* in human blood. Thus the chances of infection became so greatly lessened that the disease died out. It is clear, however, that the return of a number of infected persons from tropical malarial districts, might result in the re-introduction on a great scale of malaria into this country. Its disappearance here affords strong evidence that mosquito-borne disease may be checked without complete extermination of the insects concerned if their numbers in the neighbourhood of human dwellings be drastically reduced. This has been shown by the action of Ross and others in many hitherto deadly tropical regions, to be feasible and effective.

A large culicine mosquito, formerly known generally as *Stegomyia fasciata* but now usually referred to in entomological literature under the name *Aedes argenteus*, with a wide distribution in the tropics and warmer regions of the world, is of very great importance as the transmitter of the organism (a spirochaet) which causes yellow fever, one of the most dangerous of tropical and sub-tropical diseases. J. W. Folsom (1923) describes vividly the high mortality in the United States during the nineteenth century, over

forty thousand fatal cases being recorded in New Orleans alone. Until 1900 yellow fever was generally believed to be "due to some insidious poison borne by the air and introduced into the human body, probably through the respiratory system." Consequently efforts were made to fight the disease by "methods of quarantine, burning, and fumigation . . . that destroyed an enormous amount of property, including valuable cargoes, and paralysed the business and social activities of great cities." Such observed facts as the carriage of infection down the wind, though never for a great distance, suggested the likelihood of blood-sucking insects as transmitters, and the part played by *Aedes argenteus* was convincingly demonstrated by W. Reed in Cuba during 1900. In the succeeding year by the draining or oil-filming of the mosquitoes' breeding-places, yellow fever was definitely stamped out in Havana, which had during the nineteenth century suffered a yearly mortality often exceeding a thousand. A few years later the importance to mankind of the knowledge of the part taken by insects in carrying disease-causing organisms, was most strikingly demonstrated in Panama. For many decades work on the long-projected canal through the Isthmus had been held up, far less by engineering difficulties than by the prevalence of yellow fever and malaria among the engineers, managers, and workmen, for the "Canal zone was formerly one of the most unhealthful places on earth." By the use of proper precautions and the elimination of mosquito breeding-haunts, under the supervision of W. C. Gorgas, the total mortality among the white Americans inhabiting the zone was reduced to 9.72 a thousand, "a rate no higher than for a similar population in the healthiest localities in the United States." Few stories of human enterprise afford more convincing evidence than this of the powerful hindrance which can be offered to man's designs by the action of insects so long as their harmful influence remains unknown, or of the power of mankind to overcome such hindrance after a knowledge of its course and nature has been acquired.

The vital connection of mosquitoes with yellow fever and malaria has become known only during the present century, but it is nearly fifty years since P. Manson (1878) demonstrated that *Culex quinquefasciatus* and other allied mosquitoes harbour and transmit the larva of a threadworm, *Filaria bancrofti*, which is often very abundant in human blood, and may become fully grown and mature in man's body. Young larval *Filaria* are sucked into the stomach of the mosquito when it feeds on blood, and migrate thence into the insect's muscles and on to the base of the proboscis, so that, after some weeks' development in the *Culex* acting as an alternative host, they can be injected into the body of a human being wherein they may attain maturity. As the full-grown *Filaria* are several inches long, and produce large numbers of eggs, their presence in numbers may "obstruct the lymphatic canals and cause enormous swellings of feet, legs, and arms or other parts," symptoms of the horrible tropical disease known as "elephantiasis."

One of the most dreaded diseases that has ever affected mankind, the Oriental "Plague," which made its first appearance in Europe in the sixth century A.D., became notorious in the Middle Ages as the "Black Death," and carried off thousands of London citizens in the great epidemic of 1665, is now known to be spread largely through the agency of blood-sucking insects. Long ago Indian writers noticed that human plague was accompanied or preceded by a heavy mortality among rats, and the mention of "golden mice" as part of the offering made by the Philistines after an outbreak of pestilence recorded in the Old Testament (1 Sam. vi. 4), has been regarded by some students as indicating similar observations. The causal organism of plague, *Bacillus pestis*, a member of the bacterial group which contains many deadly germs, was not detected until the year 1894, and this bacillus was found to cause fatal "bubonic" disease in rats as well as in human beings. Very soon investigators realised the probability that blood-sucking insects were instrumental in carrying the plague organism from rats to men, and it was detected in bugs,



various flies, and most notably in fleas. A good summary account of the progress of the research, in which Japanese, French, and Russian students co-operated, has been given by H. Russell (1913), and it has been well established that the rat-flea *Xenopsylla cheopsis* is the most frequent carrier of *Bacillus pestis*. The stomachs of fleas which have sucked blood from plague-stricken rats may become densely congested with masses of the bacilli. If these fleas get on human subjects, the micro-organisms are voided by the fleas on the skin, and their bites, or the abrasion of the skin by their tormented victims' endeavour to get relief by scratching, open a way for the entrance of the germs into the human system. Fleas may also infect one human being from another, but for the continual spread of bubonic plague it seems necessary that there should be an association between the four organisms : bacillus, rat, flea, and man. When this connection is understood it is seen at once how the elimination of plague follows improved conditions of housing, sanitation, and cleanliness. It is, however, important to remember the danger which arises from the fact that the number of rats in Great Britain approaches or equals the total human population, that *Bacillus pestis* has been detected in rats in various parts of England, and that the common rat-flea *Ceratophyllus fasciatus* may serve as a transmitter.

In many parts of Europe typhus has often proved a scourge well-nigh as deadly as plague, and has been especially fatal in the crowded, unhealthy environment of oldtime camps and prisons. The part played by two species of lice (*Pediculus capitis* and *P. corporis*) infesting human beings in transmitting the micro-organism of typhus was demonstrated in 1910 by H. T. Ricketts and others. Consequently when during and after the Great War serious epidemics of typhus appeared in Eastern Europe it was realised that louse-free persons would be safe from infection, so that the medical officers of various armies and relief expeditions were able to take the necessary measures for enforcing that cleanliness which is a condition of safety.

Insects which are continually in contact with mankind may act as disease-carriers even if they do not suck blood, and this section of our subject is abundantly illustrated by the importance, now well recognised, of *Musca domestica*, the "common house-fly." Every one knows the abundance of these insects in our dwellings during the late summer and autumn months, and the manner in which they are attracted by various food-substances so that they walk over bread, butter, and meat, and frequently fall into jugs and other receptacles containing milk. Like all members of its family, the house-fly has a pair of delicate adhesive pads on each foot, so that it readily takes up material from whatever objects it may rest on. The danger of the house-fly to human health is due to its breeding habits, for the female seeks all kinds of unclean substances wherein to lay her eggs. Garden rubbish, horse-dung, and many other kinds of animal waste-matter, including human excrement if available, heaps of old rags and similar refuse—such are the objects from which house-flies come through the open window for an exploration of the breakfast-table. The house-flies' breeding haunts swarm with countless micro-organisms, and it has been reckoned that a single insect may carry a million and a quarter bacteria for dissemination among human food. It has been abundantly proved that house-flies are thus concerned in the spread of typhoid, infantile diarrhoea, and other diseases of the human digestive tract. Their harmful activity in this respect has been well demonstrated by L. O. Howard (1900), C. G. Hewitt (1914), and R. Newstead (1907), and the sanitary importance of the knowledge of the house-fly's habits and the consequences thereof has been proved by the comparative immunity from typhoid during the recent "Great War" of large bodies of troops whose medical officers acted on the ascertained facts so as to minimise the risk of infection. By screening carefully from approach of flies all refuse in which they seek to lay their eggs the insects are prevented from carrying infection to food, and it is also possible to catch and kill large numbers of flies by means of suitable

traps. In many wars of the last century, when the importance of house-flies from this point of view was unknown, armies exposed to risks of infection through the absence of sanitary precautions now regarded as essential, often suffered far more heavily from fly-borne typhoid casualties than from the attacks of the human enemy.

In closing this brief account of the action of insects as disease-carriers, the knowledge of which has become greatly increased and recognised as of high importance in our own day, it is instructive to remember that through human history insect hosts have been regarded as possibly serious

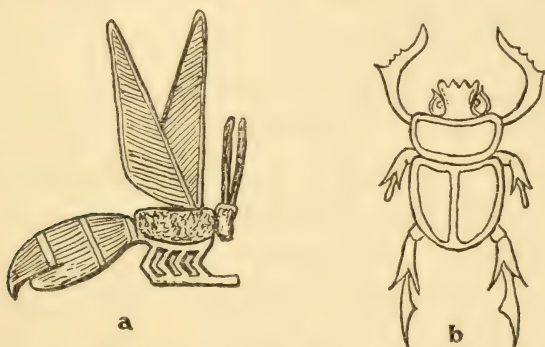


FIG. 88.—*a*, Bee, and *b*, Scarab Beetle on ancient Egyptian stone slabs in the Manchester Museum; *a*, from a Sixth Dynasty tomb (about 2700 B.C.), *b*, from an Eleventh Dynasty temple (about 2100 B.C.).

enemies of man. Not only did men dread such obvious ravagers of human food supplies as the swarms of locusts, familiar to dwellers in the Mediterranean basin around which were cradled the ancient civilisations; the Egyptians realised that flies and lice might be veritable plagues, and the "hornet" was regarded as an effective ally of the Hebrews in their attack on the Canaanites. On Egyptian inscribed stones, some of them of remote antiquity, the side view of a hymenopterous insect (Fig. 88, *a*) with uplifted wings is frequently depicted; this would be identified by many naturalists as a hornet or wasp, though it is believed by scholars to represent a bee. It is of great interest,



however, to find that this insect is the symbol of the ancient kings of Lower Egypt, and it might be regarded as suitable that a creature provided with a formidable sting should stand in the hieroglyphs for a monarch powerful in war. Flies are also depicted on the Egyptian monuments and represented in amulets; possibly this latter custom may indicate some suspicion of the connection between insects and human diseases.

Much of this chapter has been devoted to the subject of insects that are in various ways harmful to man's agricultural and other industries as well as to his bodily health. It is only fair, as we draw to a close, to pay some attention to the insects which may be regarded as beneficial. Incidentally it has been pointed out how insects that ravage farm crops and garden plants and trees are preyed upon or parasitised by other members of the class. Thus, leaf-eating caterpillars are pursued and eaten by predaceous beetles, hunted by digging-wasps and buried as a provision for their offspring, or devoured internally by the grubs of ichneumon-flies. The common "Cabbage White" butterflies (*Pieris*) are kept in check by the small ichneumonoid (Braconid) fly *Apanteles glomeratus*, whose white grubs, when fully grown, make their way out of the Pierid caterpillar in which they have fed (Plate XI, B) and spin their oval, yellow cocoons around its dried cuticle. Plant-sucking insects, such as aphids and coccids, are destroyed in large numbers by ladybird-beetles and their grubs, by the larvae of lacewings, and by the active maggots of the hover-flies. We have seen how the result of the activities of such predaceous insects has been demonstrated by their introduction from one continent to another in order that they may be used by human cultivators for the control of pests, which have themselves been inadvertently introduced.

Quite a large number of insect species in various parts of the world have been brought in some way into the direct service of mankind. Some races of men, for example, habitually eat insects. According to D. Sharp (1899) an Australian owl-moth, *Agrotis spina*, the Bugong, "occurs in

millions in certain localities in Victoria ; . . . it formed an important article of food with the aborigines." Termites are eaten by hill-tribes in India and by other primitive races ; certainly a queen-termite with her thousands of contained eggs must be admitted to furnish a highly nutritious form of diet. Large grasshoppers and locusts have been eaten from early times in the Mediterranean basin as well as in North America, where some of the tribes of Redmen, according to Folsom, regarded as " especially delicious . . . a bushel of grasshoppers roasted in a hole in the ground." J. M. Aldrich describes how an Indian tribe of California gathers every other year to collect the large pine-feeding caterpillars of a saturnid moth, *Coloradia pandora*. These, dried and preserved for eating, are said to taste like linseed oil. While the use of insects themselves as food has never been practised by a large proportion of the human race, the insect-product honey has served as a valued food in almost all parts of the world among all races through thousands of years of human history.

Reference has already been made to the acquaintance with the bee displayed by the ancient Egyptian sculptors and scribes, who took the insect as a symbol of royalty. It is well known that the mother of a bee community was until a century and a half ago regarded as a male and described as the " king " of the hive, or as in Shakespeare's familiar description (*Henry V.* 1), the

" . . . emperor  
Who, busied in his majesty, surveys  
The singing masons building roofs of gold,  
The civil citizens kneading up the honey,  
The dull mechanic porters, crowding in  
Their heavy burden at the narrow gate."

Through the long centuries when the sugar-cane was unknown to the peoples of Europe and the Mediterranean basin, the honey of bees was the source of all luxuriously sweet food. It is no wonder therefore that the honey bee was highly valued by the ancients, communities of these insects being domesticated and preserved in hives several

centuries at least before the Christian era, for the sake of their sweet product. Where *Apis mellifica* was not domesticated, men sought out the combs of various species of *Apis* and, like the prophet of the Judæan wilderness, fed gladly on "wild honey." The constant association of sweetness with the hive-bee's product is well illustrated by an expression used when, through the Indian expedition of Alexander, cane-sugar became known to the Greeks; it was stated that the Macedonian conqueror had fed on "solid honey not made by bees." It is of interest to find that swarms of domesticated bees, if not provided with new hives, may establish themselves in hollow trees or similar situations, thus demonstrating the capacity of the species to revert to an independent life notwithstanding its long association with mankind. The wax secreted by bees is a product of considerable value to man in addition to their honey; beeswax is used for the manufacture of polishes, varnishes, and ointments as well as by sculptors for modelling and for dentists for taking moulds of their patients' palates and gums. It is interesting to remember that some wax is returned as a labour-saving device to the bees, in the "artificial foundation" provided for the construction of the comb in the wooden frame-hives, now generally used by modern bee-keepers.

After the hive-bee the most familiar and important of domesticated insects are the "silkworms," caterpillars of *Bombyx mori* and of various species of Saturniidae, whose cocoons are constructed of pure silken threads which can be unwound, and used for spinning the material of which silken fabrics are woven. The "Common Silkworm" (*Bombyx mori*) was cultivated in China before the year 2500 B.C., and until comparatively recent times no other species was used as a source of silk for use in manufacture. After the eastern conquests of Alexander silken fabrics became known to the Greeks and Romans, but the production of silken thread was a monopoly of the Far Eastern peoples until the sixth century A.D., when returning monks brought cocoons of *Bombyx* to Constantinople. The moths



reared from these were utilised to start silk-cultivation in the Mediterranean countries, the industry passing westward to Italy in the twelfth and to France in the sixteenth century. The prolonged domestication of *Bombyx mori*, which is unknown in the wild state, has been accompanied by remarkable degeneration both in the moths and caterpillars. The former are incapable of flight, and the larvae, as J. H. Watson (1911) has pointed out, lose after their first moult the dark colour and strong hairy clothing characteristic of their family and become pale, feeble, and almost naked; while the legs are abnormally reduced, "their grasping power so small that it is insufficient to sustain the larva when held upside down on a leaf and gently shaken." Fed in its domesticated condition on leaves laid flat on trays, the silkworm is incapable of climbing on twigs, so that "were it put in the open on the mulberry trees it would starve in the midst of plenty, not having strength to climb about for its food as wild species must do." Naturalists who accept the action of the Lamarckian factor in evolution would naturally explain these degenerative changes as definitely induced by the conditions of domestication. Certainly they must be regarded as accompaniments of the silkworm's age-long association with human industry. The large spiny caterpillars of several species of Saturniid moths have been successfully reared for silk-production for many years past; of these the best known is *Antheraea mylitta*, an Indian moth whose cocoon is the source of "tussore" silk, and *A. pernyi*, a Chinese species cultivated for the "Shangtung" silk. Watson suggests that the Saturniidae might prove "a sheet anchor in the case of the failure of the production of silk by *Bombyx mori*." The modern textile experts have, however, produced another possible "sheet-anchor" in the now familiar "artificial silk," the fibres of which are drawn out from wood-pulp.

Another group of insects which have for long been utilised by man are those Coccidae which produce lac, the resinous substance whence various varnishes, including shellac and lacquer, are made; the names of these indicate


the source of their chief ingredient. The typical lac insect (*Tachardia lacca*), which has been fully described by A. D. Imms and N. C. Chatterjee (1915), inhabits large tracts of India and Burma, and is found on a great variety of trees which "contain a gummy or resinous fluid or are rich in latex"; thus material is provided for the epidermal secretion which hardens to form the lac or protective "scale" covering the body of the mature female. The name "lac" ("lakh" in Hindi), which can be traced back to Sanskrit, means a hundred thousand, "in allusion to the multitude of larvae of the insect that are present during the period of larval emergence." The various forms of *Tachardia lacca* are bright red in colour, and the name reappears in the artist's crimson "lake," a pigment extracted from the insects' bodies; the insect-origin of this colour was known in Europe seventeen hundred years ago. *Tachardia* is preyed upon by a great variety of insects, the most formidable being the caterpillars of the noctuid moth *Eublemma amabilis*; a heavy mortality follows naturally because the prolific reproduction of the lac insect provides abundant food for its enemies, so that these can multiply at a rate which threatens at times to exterminate their victims, a result which on account of the economic value of *Tachardia* would be deplored by cultivators. In this instance the predaceous insects are reckoned to be harmful, whereas most creatures which devour Coccidae—a family on the whole distinctly destructive—are hailed by mankind as benefactors.

Examples of the relations between insects and mankind have now been given in sufficient number to illustrate how various in their nature and in their effect on human life such contacts are. When we think of the myriad insects that devour crops, live as parasites in or on domestic animals, invade man's own body, suck human blood and inoculate his system with germs causative of dread diseases, it may seem fitting that the name of the old Eastern divinity who was worshipped as Baalzebub, the "Lord of Flies," should have been transferred later to the author of evil. But we

have seen how the harmful effects wrought by insects often follow inevitably from human activity in cultivation and domestication, and how these effects have themselves stimulated man to inquiry and thus to the attainment of knowledge through which preventive and remedial measures have been indicated. And thus we realise that there was justification for the hopeful vision of Joel, who, using the destructive locust-swarms of the Mediterranean coast-lands as symbols of ravaging armies, recognised them as working out ultimately a beneficent purpose, and held to the faith that "the years which the locust and the caterpillar had eaten" should be in due time restored.

Many insects are, as we have seen, definitely serviceable to man, by acting as scavengers, by preying on the destroyers of crops, and by furnishing useful products such as honey and silk. The most valuable contribution, however, which insects as a class have made to the well-being and enjoyment of mankind, is undoubtedly to be seen in the result of their association with the higher seed-plants, apparent in the colour and scent of flowers, and the development of the fruits of plants dependent for pollination on insect visitors. The world into which man came would have been far less attractive and sustaining than he found it, but for the interactions which had gone on between the higher insects and the plants through the later Secondary and the Tertiary eras of geological history.

Yet beyond these considerations insects have been a means of benefit to man through their direct appeal to his love of beauty and his search for truth. The student of these creatures finds beauty not only in the brilliant hues of a butterfly's wing or the metallic sheen of a beetle's elytron, but also in the wonderfully adapted form of those minute organs and structures which subserve the needs of life; graceful feathered feelers that are the seat of delicate sense-organs, claws and pads on feet that ensure firm hold in walking—all might well be acclaimed as "miracles of design." We have seen how the study of insect structure and development has thrown light on the problems of





heredity and evolution that have a bearing on the history of all living creatures in the world. Then the study of insect behaviour affords instructive examples of the working of inherited reflex actions for the benefit of the family, the society, and the race, while in many cases there is clear indication of memory and intelligence.

In our discussion on Insect Behaviour (Chap. V) allusion was made (pp. 94-95) to the way in which writers of various nations and periods have held up the behaviour of ants and bees as an example to human communities. Many of the activities of such insects have indeed a resemblance to those of man, and the ordered industry of the ants' nest or the bee-hive may be used to emphasise the importance of service to the common good. Yet the student of insect life who thinks at times about the problems of human society, cannot accept the great family-state of the ants, bees, or termites, with its predominantly automatic activities and its complete subordination of the individual, as a model for his own commonwealth. It will be remembered that the familiar passage from Shakespeare's *Henry V.* quoted a few pages back, occurs in a speech advocating "obedience" as the end of national purpose, even if called out by the resolve of an ambitious ruler to embark on aggressive war. The analogy of the hive in such an argument depends largely on the supposed monarchical system of the bee community, and we now know well that the "queen," so far from directing the activities of the workers, is herself controlled by them. The organised insect society is splendidly efficient because its multitude of members have the innate tendency to respond accurately to the successive stimulations of their environment, material or animate. The result is an apparent communistic purpose leading to activities in which the individual has neither initiative nor responsibility. Despite the superficial likeness, nothing could be more diverse fundamentally from a human commonwealth, whether its members obey the orders of a despotic ruler, or by way of discussion and reasoned action work willingly for the general good.

The study of insect life, with its definite practical and intellectual appeals to those who pursue it, is not devoid of spiritual aspect. The ancient Egyptians, who used the bee as a symbol of their king, paid divine honour to representations of the dung-beetles (*Scarabaeus*), and laid the image (scarab) of the creature to replace the heart of the mummified dead. According to E. A. W. Budge (1925) and other archaeologists, the beetle's action in rolling over and over the ball of dung which serves it for food-supply, suggested to primitive observers the revolution of the sun in the heavens, and thus the beetle became a symbol of Kheper, the creator who made and sustained in their courses the celestial spheres, and caused the sun to rise again after each evening's setting. As a natural further step in symbolism, "the ideas of resurrection and renewed life became associated with the beetle." The use by the Greeks of the same word ( $\psi\upsilon\chi\eta$ ) to designate a butterfly and the soul shows how the well-known transformation from crawling caterpillar to winged imago seemed a parable of man's higher nature, so that to them also insects became silent prophets of immortality. Not to pagans only did this symbol from insect life-history appeal; it was taken up by the great seventeenth-century Dutch zoologist Swammerdam as an illustration of the Christian doctrine of the future: "we see therein," he wrote, "the resurrection painted before our eyes." It is noteworthy that Swammerdam was a pioneer in the elucidation of the true nature of insect metamorphosis, for he saw the preformation of imaginal rudiments in the larva, and realised the individual continuity of life through all stages of growth; the modern student of things natural and spiritual may find the parallel no less attractive on that account.

While such analogies are of interest as showing how details of insect development and behaviour have drawn out the deeper aspirations of various observers, there is a more compelling appeal in the wide vision of purpose which the study of insects, as of all nature, reveals to those who, in the true scientific spirit, seek for a reasonable

explanation of the facts which they observe. The insects present to us an immense multitude of various forms, differing among themselves in structure, life-history, modes of behaviour; to attain an imperfect knowledge of one group demands the careful labour of years, and the worker realises with each advance how much more remains to him unknown. Yet he doubts not that knowledge is possible, not only a knowledge of facts that can be seen and set out in orderly sequence, but an increasing understanding of the processes by which these millions of small living creatures work out their life-relations, and how through the long ages of the earth's history they have come to be as they are. The scientific worker does well to be humble in face of the vast unknown, while he trusts continually that the scheme of nature is reasonable and intelligible. The rational justification for scientific inquiry is really a faith that the Eternal Mind working through nature is akin to our minds and, even through the study of insect life, man may be called anew to worship as well as to wonder and admire.



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